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ASSESSING RANGELAND RESILIENCE TO HERBIVORY IN

ELK ISLAND NATIONAL PARK

by

Jody Nicole Best © Ⓒ

A thesis

submitted to the Faculty of Graduate Studies and Research

in partial fulfillment of the requirements

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled 'Assessing Rangeland Resilience to Herbivory in Elk Island National Park' submitted by Jody Nicole Best in partial fulfillment of the requirements for the degree Master of Science in Rangeland and Wildlife Resources.

ABSTRACT

Continuous and intense native ungulate herbivory has changed plant community composition and structure in Elk Island National Park (EINP). To assess community recovery six ungulate-proof exclosures (20 by 50 m) were constructed during 1998-99 enclosing forest and grassland communities. Physical site characteristics, overstory parameters, plant species composition, herb standing crop and shrub current annual growth were measured in 1999 and 2000 to assess short-term rangeland resilience following herbivory. While the removal of herbivory increased shrub height and cover, as well as herb standing crop, exotic and native species cover did not change appreciably on protected sites, with invasive species continuing to dominate grasslands. In an additional investigation of transplanted *Festuca hallii* (Vasey) Piper plants in grasslands grazing was found to reduce fescue survival and tiller growth. In a study of the shrub *Corylus cornuta* Marsh, shrub stems responded variably among exclosures, but generally supported the hypothesis that ungulate browsing reduces long-term growth. These results indicate the short-term resilience of plant communities in EINP is low and native plant communities may not recover from heavy grazing for several years without active rehabilitation and that herbivory may have to be reduced to promote native species recovery.

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CHAPTER 1: Introduction

National parks are lands federally legislated by the National Parks Act, with the mandate to "protect and preserve ecological integrity and biodiversity for future generations, public education and enjoyment" (Parks Canada 1988). Despite this mandate, national parks have a history of managing for key animal species, and ignoring ecosystem processes (Ovington 1984). To better fulfil the requirements of the National Parks Act, many park managers are starting to focus on the preservation of ecosystem processes in order to conserve habitat and wildlife together.

Conservation, use and development of adequate habitat are probably the most important factors affecting wild ungulate management (Scotter 1980). Hanson and Smith (1970) identified supply and maintenance of quality forage as one of the most challenging influences on wildlife production. Wildlife depend on vegetation for food and shelter (Odum 1997; Bishoff 1981; Hanson and Smith 1970), and may in turn, influence habitat dynamics (Frank 1998). Rangeland ecosystems have evolved under the influence of disturbances and are well-adapted to tolerate moderate levels of herbivory. In fact, the removal of grazing has been observed to de-stabilize some ecosystems (West 1993). Intense herbivory on the other hand, may be detrimental to rangeland plant communities (Wambolt 1998; Bork et al. 1997b; Willms et al. 1985; Mueggler 1985; Mitchell and Cormack 1960).

Located near Edmonton in east-central Alberta, Elk Island National Park (EINP) is a highly productive ecosystem capable of rapid vegetation succession, and supports a variety of ungulates (Blyth 1995; Bishoff 1981). The Park is home to some of the greatest densities of free-ranging ungulates in North America (Parks Canada 1999; Telfer

and Scotter 1975). Since the Park's inception in 1906 and the eradication of major predators, Park managers have employed several strategies to control ungulate populations, including slaughter, self-regulation, and more recently, live-trapping for relocation to other areas (Parks Canada 1999; Blyth 1995). However, high ungulate numbers persist, and rangeland condition has declined.

Herbivory has been documented as heavily impacting plant community composition (Bork et al. 1997a), as well as vegetation diversity, structure, and productivity within the Park (Bork et al. 1997b). These ecological changes are likely the result of EINP's small size (194 km^2), fenced perimeter, and high ungulate populations over the past several decades. In general, localized intensive herbivory has reduced the height of the understory, resulting in a shift within plant communities towards shorter, more grazing tolerant herbs and shrubs (e.g., *Corylus cornuta* Marsh.), and a greater abundance of introduced (e.g., non-native) species. These changes are particularly evident on south-facing slopes within the Park, which have been referred to as "grazing lawns" (Bork 1993). These sites, which presumably supported native species such as plains rough fescue (*Festuca hallii* (Vasey) Piper) in the past, are now dominated by Kentucky bluegrass (*Poa pratensis* L.) and dandelion (*Taraxacum officinale* Weber), with plains rough fescue now found at only isolated locations. In addition, mature specimens of palatable shrubs such as saskatoon (*Amelanchier alnifolia* Nutt.) and chokecherry (*Prunus virginiana* L.) are nearly absent in the Park, and aspen regeneration has been severely limited (Bork et al. 1997b). Many of these ecological changes are in conflict with EINP's mandate to preserve the area's ecological integrity and its inherent natural biodiversity.

In August of 1997, a workshop was held to address the future management direction of EINP. Arising from the workshop were several management changes for the Park, including the establishment of three discrete Land Management Units (LMU). These units represent a gradient from open aspen parkland in the south, through moderately forested parkland, to nearly continuous boreal forest in the north (Equus Consulting Group Inc. 1997). Other recommendations included: (1) the restoration of fire to re-establish the aspen parkland – boreal transition, (2) a further evaluation of the impact ungulate populations have within EINP, particularly with respect to the Park's ability to maintain ecological integrity (e.g., natural components and processes), and (3) a reduction of ungulate numbers in an effort to improve range condition. It was also recognized that no information existed on the potential resilience of the Park's rangelands to a change in native ungulate numbers and associated herbivory. This information could be obtained through the establishment of rangeland reference areas.

As a result, a research program was initiated in the fall of 1998 to evaluate the response of EINP rangelands to the removal of ungulate herbivory. To accomplish this, six permanent rangeland reference areas (e.g., exclosures) were constructed in the winter of 1998-99 to form the basis of a long-term monitoring program for Park habitat and facilitate research into rangeland recovery. Specific objectives of the research described here were to: (1) assess the short-term changes in species composition, community diversity, vegetation structure, and productivity following the removal of herbivory, and (2) determine how changes in rangeland vegetation characteristics [listed in (1)] may vary between forested and grass/shrubland plant communities within the Park. Additionally, the exclosures formed the basis for evaluating the intra-specific responses of two

important native plants, *Festuca hallii* and *Corylus cornuta* Marsh., to the removal of

herbivory within the Park.

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CHAPTER 2: Literature Review

2.1 Introduction

Ecology is the integrated study of organisms, the physical environment and human society (Odum 1997). Conservation ecology is mainly concerned with wildlife and habitat management. While ecologists study many levels of the ecological hierarchy from populations to communities to ecosystems and landscapes, one persisting challenge has been the monitoring of range condition, and ecosystem health or ecological integrity (NRC 1994).

Traditional range monitoring methods use plant community composition and production to assess range condition. Biodiversity is often used to evaluate the long-term trends of rangeland condition. West (1993) defined biodiversity as the variety of life and it's processes; a multifaceted phenomenon involving the variety of organisms present, the genetic differences among them, and the communities, ecosystems, and landscapes in which they occur. West (1993) noted that biodiversity is a hot topic of discussion due to the threat of global environment change, accelerated species extinctions, and changing societal values, which collectively continue to increase the importance of ecological monitoring.

While many studies have used biodiversity and more specifically, species diversity, to evaluate range condition and trend (Gaston 2000; Purvis and Hector 2000), some suggest that diversity alone may not be the most accurate indicator of ecosystem health (Collins 2000; Wicklum and Davies 1995). Tilman (1996) found that biodiversity stabilized community and ecosystem processes, but not population processes that

fluctuated greatly due to inter-specific competition. At the ecosystem level, a loss of biodiversity may result in reduced ecosystem stability and function (Tilman 2000). Yet other studies indicate that knowledge of temporal dynamics is necessary before community or ecosystem stability may be evaluated (Collins 2000; Gaston 2000).

There are many ways to measure biodiversity. However, all methods are value-laden, as the choice of variables to measure depends on what is important to human society (Wicklum and Davies 1995; West 1993). It has been suggested that the maintenance of ecosystem processes and soil conservation are probably more important than the retention of individual species (West 1993). Ideally, several ecosystem characteristics and processes such as diversity, production, structure, watershed function, disturbances, and nutrient cycling should be monitored simultaneously at various temporal and spatial scales in an effort to evaluate ecosystem quality and sustainability.

2.2 Grazing Ecology

Disturbance is a common and necessary part of the complex processes of natural ecosystems (Maini and Carlisle 1974). Changes to disturbance regimes resulting from human interference may alter species abundance and occurrence, as well as ecological processes within a given system (West 1993; Hobbs and Huenneke 1992).

Beetle (1974) suggests that the dominant grazing ungulate is the apex of the food chain, and the only element in the habitat worthy of consideration if one wants to preserve representative natural environments and native biota as integrated wholes (e.g., ecosystems). On the other hand, West (1993) challenges land managers to work to

sustain soil and ecosystem processes, rather than specific species, in order to preserve natural environments.

2.2.1 Plant Response to Herbivory

Disturbances such as grazing and fire affect plant growth and the use of non-structural carbohydrates, changing plant survival (Bedunah and Sosebee 1995). Most plants are adapted to and tolerant of, the periodic herbivory experienced under the grazing habits of native ungulates such as bison and wapiti. It appears native plants are less adapted, however, to the frequent, heavy defoliation often found in systems where the natural migration patterns of ungulates have been disrupted, and plants are not afforded time to recover between defoliation events (Bork 2000). Ultimately, ecosystem management for grazed/browsed systems should balance animal use with plant tolerance and recovery.

Plant survival depends on the continued synthesis and storage of energy, maintenance of a healthy root system, and periodic reproduction. Grazing tends to increase several processes, including the photosynthetic rate of remaining tissue, the allocation of current photosynthates to new shoots, the relative allocation of substrates from roots to shoots, and in grasses, tillering (Belsky 1986; Richards 1984; Detling et al. 1979). Light grazing causes a reduction in leaf area that temporarily slows or stops root growth (Bedunah and Sosebee 1995), but plant respiration requirements are easily met and new leaf growth is promptly initiated. Upward mobilization of carbohydrates lasts only 4-5 days after an episode of herbivory and these carbohydrates are quickly replaced. In contrast, severe or heavy grazing typically reduces leaf litter and plant growth while

increasing root death (e.g., Johnston 1971, 1961). Eventually, carbohydrate reserves are severely depleted and phenological functions such as seed set impaired. If extremely heavy grazing pressure occurs, plant death may occur from the unrecoverable loss of leaf area and carbohydrates.

In general, plants have two adaptations to deal with herbivory: avoidance and tolerance/resistance (Holechek et al. 1998; Bedunah and Sosebee 1995). Some plants may decrease in abundance even at low levels of herbivory because they are either intolerant of grazing or may be highly preferred (e.g., selected) forage species. In contrast, other plant species may increase under grazing because they are relatively tolerant to use or less frequently defoliated (Bedunah and Sosebee 1995).

Plants that avoid grazing use mechanical or chemical means to deter herbivory (Radwan 1974). Mechanical avoidance strategies include the use of thorns, awns, or thick, woody tissue to reduce herbivory. These species include wild rose (*Rosa woodsii* Lindl.) and raspberry (*Rubus* spp.). Plants using chemical means to avoid herbivory produce unpalatable or toxic substances. These forbs and shrubs include species like water hemlock (*Cicuta* spp.) and chokecherry (*Prunus virginiana* L.), and others that produce alkaloids, cyanogens, tannins, resins, or waxes to render themselves less palatable. Plants that avoid grazing forsake some growth and reproduction by using energy to produce these specialized structures and/or chemicals.

In contrast to avoidance, plants may also tolerate herbivory. These plants protect themselves through a variety of mechanisms. Some species minimize access to apical meristems by keeping them near or below ground level (e.g., short internodes in grasses). Many grasses do not rely on seeds for reproduction, but reproduce mainly via rhizomes,

stolons, or tillering, thereby ensuring propagation. Grass species that do rely on seeds to reproduce elevate their seed heads quickly to reduce seed exposure to herbivory. Still other species store high levels of carbohydrates in their roots to facilitate rapid regrowth following defoliation.

Defoliation of shrubs removes apical dominance, or the terminal growing point of the plant. This triggers lateral bud release, which may produce more twigs (Bedunah and Sosebee 1995). Resprouting after defoliation, as seen in many boreal shrubs and trees, rapidly restores photosynthetic area for prompt recovery. Carbohydrate stores in the roots are mobilized and used for re-growth. If shrubs are browsed predominantly in the winter they may use the summer growing season to recover and replenish carbohydrates, and thus, be less detrimentally affected than if browsed during the summer growing season. Defoliation during the growing season reduces a plant's ability to store carbohydrates and, depending on the level of defoliation (light to heavy), may reduce the sexual reproduction potential of the plant (Bedunah and Sosebee 1995).

2.2.2   Plant Community Responses to Herbivory

2.2.2.1 Community Diversity & Structure

The intermediate disturbance hypothesis (IDH) suggests that physical disturbance at moderate levels may maximize diversity by reducing competitive exclusion (Wootton 1998; McIntyre and Lavorel 1994; Hobbs and Huenneke 1992; Grime 1979): the absence of disturbance reduces species diversity by allowing one species to monopolize resources. Similarly, high levels of disturbance decrease species diversity because some species

cannot reproduce fast enough to compensate for increased mortality (Wootton 1998; Tilman 1996). Milchunas et al. (1988) suggest that the IDH is most likely to apply in rangelands where precipitation is relatively abundant and vegetation is well-adapted to tolerate historical levels of herbivory. Disturbance may also increase diversity by altering the nature and availability of micro-sites (Hobbs and Huenneke 1992).

The IDH has been widely accepted. However, Wootton (1998) suggests that although basal species in the food web are likely to follow IDH theory, top consumers are not. Wootton (1998) argues that the application of IDH has usually been limited to one trophic level and may not be accurate for whole ecosystems. In addition, disturbances ultimately interact with other ecological processes to affect observed patterns of species abundance and diversity (Wootton 1998; McIntyre and Lavorel 1994).

Herbivory may alter the appearance, productivity and composition of plant communities. For example, Hartnett et al. (1996) observed that, in addition to increasing diversity, the cover and frequency of cool season grasses and select forbs were consistently greater on grazed sites, while grazing decreased the cover of dominant warm season grasses. Other studies have found that grazing may increase the relative abundance of exotic and unpalatable species (Kay and Bartos 2000; Willoughby 1998; Rosenstock 1996; Trottier 1986; Mueggler 1985; Polster and Watson 1979). Kentucky bluegrass is an exotic species known to increase under continuous heavy grazing, and has become an indicator of intense herbivory (Tracy and Sanderson 2000; Shulz and Leninger 1990).

In addition to changes in species composition, grazing may alter plant community structure. Moderate grazing may result in an increase of woody plants in grasslands by

eliminating competition for water and nutrients from the herbaceous understory (Archer et al. 1988). Conversely, if areas are grazed/browsed severely for extended periods of time, plant death is inevitable, bringing with it changes in plant species composition and community structure. If these conditions persist, in addition to plant community changes, a feed emergency may occur. Beetle (1974) suggests that one indication of a feed emergency is the presence of a browse line where vegetation is repeatedly clipped to a consistent height and less palatable species are often consumed. In these situations browse species may be held in an early stage of growth by herbivores, potentially weakening the plants over time. Continuous browsing will reduce plant growth and root activity, and other species may invade the site. For example, areas previously covered by shrubs may revert into grassland (Bailey et al. 1990; Field and Ross 1976), or a native grassland may be overtaken by more grazing tolerant, introduced species (Trottier 1986). Deer browsing has also been found to reduce the availability of shrubs and tall forbs, while increasing grasses (Kay and Bartos 2000). In some cases, deliberate intensive browsing of woody species has been used to control the amount of tree growth and establishment (Bailey et al. 1990). Since the effects of herbivory are plant species specific and often depend on the herbivore involved, managers frequently need to decide which taxa to manage for (Hobbs and Huenneke 1992).

2.2.2.2 Production

All rangelands have evolved under the effects of herbivory and other disturbances (Holechek et al. 1998). West (1993) suggests that the removal of grazing may destabilize some ecosystems. Light to moderate grazing may increase the production of a plant

community by removing excess litter and plant material (Frank 1998) or stimulating tiller development (Wan and Sosebee 2000). In addition, frequent light grazing may maintain plants in a more vegetative state, thereby increasing the quality and season-long accumulated quantity of forage available to herbivores (e.g., compensatory growth) (Bedunah and Sosebee 1995). Heavy grazing on the other hand, typically reduces forage production, as well as increasing inter-annual variation in production (Bork 2000; Tillman 1996; Willms et al. 1985; Smith 1952).

Similar to plant community diversity and structure, the effects of herbivory on production depend on the plant species involved, as well as the physical site characteristics and type of herbivore (Hobbs and Huenneke 1992). For example, low intensity bison grazing has been found to enhance soil water availability and associated forb productivity within grazed patches (Fahnestock and Knapp 1994).

2.2.2.3 Range Condition

Succession refers to the process of one plant community replacing another until a final stable climax community is achieved (Holechek et al. 1998). Climax is the final stage of succession and can be defined as the plant community that might occur in the absence of herbivory, given the location's range site potential. Any disturbance (e.g., grazing, fire, drought) may cause retrogression within the plant community towards a lower seral state.

Range condition assessment evaluates the effects of management practices (e.g., grazing, fire) on rangeland vegetation. It also facilitates the detection of temporal changes that occur naturally within rangelands. Traditional methods of condition

assessment have been based on the linear model of vegetation succession (Clements 1936). This method compared the climax (or potential natural) community to the current plant community (Dyksterhuis 1949), with greater deviations from climax indicative of poorer condition. Although this method of range condition assessment has proven useful, it does not accurately describe ecosystem dynamics and is less applicable to forested rangelands (West and Smith 1997; Lockwood and Lockwood 1993; Laycock 1991; Friedel 1991; Westoby et al. 1989). In addition, this model assumes that the climax community is the most desired plant community. This may not be the case, however, depending on management goals (e.g., species diversity, forage production, etc.).

Recently, other models of rangeland ecosystem dynamics have been developed in an effort to account for unpredictable, discontinuous changes in vegetation. Of these, the State-and-Transition model is the most popular (Westoby et al. 1989). It describes a set of stable vegetation states separated by thresholds between states (Laycock 1991; Friedel 1991). Transitions between states may be triggered by natural events or management actions capable of exceeding inherent thresholds. In this model, rangelands do not necessarily undergo orderly natural succession to climax following the removal of disturbance (Lockwood and Lockwood 1993).

While the State-and-Transition model may be more representative of ecosystem dynamics, methods for quantitative assessment of rangelands using this model are relatively undeveloped. Some ecologists now advocate the use of desired plant communities (DPC) in place of climax (West and Smith 1997). The DPC may be based on what is sustainable on a given range site, and management goals (West and Smith

1997). However, DPCs may coincide with early seral stages where production is greater and invasive plants thrive.

2.2.3 Foraging Strategies

Foraging pressure depends on site factors such as soil type and topography, as well as the type of vegetation, season, forage availability, herbivore species, and feed nutrient levels (Feist 1998; Bailey et al. 1996). Wallace (1995) observed that ungulates feed randomly within forage patches (fine scale), but may select feeding sites based on forage abundance at broader, landscape scales. In addition, forage availability is limited by winter snow cover. The Boom and Bust Theory, as illustrated by Bobek et al. (1983), suggests that ungulate populations will grow until no resources are left, and then experience a drastic decline.

Bison are considered to be relatively unselective grazers. This allows bison to utilize available forage more completely than other herbivores. Reduced dietary quality is compensated for by increased consumption (Hawley 1978), which is achieved through large bite sizes and rapid bite rates (Hudson and Frank 1987). Bison prefer grassland habitats, choosing a diet composed mostly of sedges and grasses (Telfer and Cairns 1979; Reynolds et al. 1978). Bison consume relatively little browse in comparison to species such as wapiti or deer, although plant species such as willow (*Salix* spp.) may comprise as much as 2% of the bison diet (Reynolds et al. 1978).

Wapiti are mixed or intermediate selectors because they can adjust to a grass, forb, or browse diet (Knight 1970). Morgantini and Hudson (1989) observed a seasonal cycle in elk diets: summer diets in alpine areas consisted of willow while fall, winter and

spring diets were almost completely grasses and sedges. Other studies indicate that elk prefer to graze and forage mainly on grasses and sedges when they are available (Gates and Hudson 1981; Hansen and Clark 1977).

White-tail and mule deer have been classified as concentrate selectors (Hofmann 1985). Concentrate selectors typically have smaller, simplified rumens, and select feeds of higher quality (Feist 1998). Both white-tail and mule deer have been documented as preferring browse throughout most of the year (Goodwin 1975; Allen 1968; Loveless 1967).

Moose are also concentrate selectors, and prefer the browse of forest and shrubland habitats during most of the year, feeding on aquatic vegetation only during the early summer (Bishoff 1981). Moose production has been positively correlated with browse production in 3 areas of Alberta (Telfer 1978). Moose in the Northwest Territories preferred certain willow (*Salix* spp.) and other species whose morphology was influenced by previous browsing (Penner 1978).

2.3 Beaked Hazel Ecology

Beaked hazel (*Corylus cornuta* Marsh) is a shrub found in southern portions of the Boreal Forest and throughout the Aspen Parkland (Kurmis and Sucoff 1989). Hazel has a great influence on forest ecology. In particular, dense hazel understories limit tree reproduction and compete with other shrub species by reducing the intensity of light reaching the forest floor (Tappeiner 1979; Tappeiner and Alm 1975; Tappeiner and John 1973).

While most beaked hazel biomass is above-ground in dense shrub layers, as much as 31 to 39% of hazel biomass may be below-ground (Tappeiner and John 1973). Most roots and underground stems are found within the top six inches of soil (Johnston and Woodard 1985; Buckman 1964), and Tappeiner (1971) observed that most underground stems occur beneath the litter at the soil surface.

Beaked hazel shrubs may reproduce by cloning. Cloning takes place after a hazel shrub has reached approximately ten years of age (Tappeiner 1971), and is facilitated by underground stems, which produce new aerial stems and roots along their length. These stems vigorously resprout in the event of disturbance (e.g., fire or herbicides) provided the underground shrub biomass survives (Tappeiner and John 1973). Death of hazel clones occurred only when below-ground biomass was killed by intense fire or herbicides.

It has generally been assumed that cloning is the main reproductive strategy for beaked hazel. However, Tappeiner (1971) found that hazel clones in northern Minnesota were relatively small (most were between 1.2 and 1.8 m in diameter), and reproduction occurred mainly from seedlings. Maximum seed production occurred when shrubs were roughly ten years old, with good seed crops limited to every five years on average (Tappeiner 1971).

Dense beaked hazel understories are usually formed by intermixed clones of various ages (Tappeiner 1971), with persistent populations dominated by young stems that increase in proportion as the hazel stand ages, eventually choking out tree seedlings and other shrubs (Kurmis and Sucoff 1989). As the tree overstory eventually matures, hazel phytomass in the understory increases (Tappeiner and John 1973) but hazel density

decreases (Kurmis and Sucoff 1989). This response to forest succession may be the result of increased overstory shading.

In addition to competing effectively with other shrub species, beaked hazel has the potential to alter litter and soil composition, as well as nutrient cycling. Tappeiner and John (1973) found that 30% of total plant nitrogen, 36% of potassium, 60% of calcium, and 10% of magnesium was stored in the leaves. These high nutrient concentrations were transferred to the litter layer on the forest floor, but did not affect mineral soil composition due to rapid litter turnover rates (Tappeiner and Alm 1975).

Tappeiner (1979) suggested that historically, beaked hazel populations were controlled by fire. With the suppression of wildfire after European settlement, beaked hazel communities invaded into areas suitable for encroachment. Several studies have been conducted to evaluate methods for controlling hazel to improve wildlife habitat and the abundance of more preferred browse species (Johnston and Woodard 1985; Tappeiner 1979, 1971; Tappeiner and John 1973; Krefting and Hansen 1969; Buckman 1964). Of these methods, fire and herbicides were the most commonly employed.

Johnston and Woodard (1985) noted that the aerial stems of hazel were very susceptible to fire, and a single burn late in the growing season could be used to kill above-ground phytomass. These results are corroborated by Tappeiner (1979) and Buckman (1964). However, more intense fires, and often multiple fires, were required to kill underground stems and prevent resprouting (Johnston and Woodard 1985; Buckman 1964).

Herbicides have proven more reliable for killing beaked hazel and facilitating the release of preferred shrub species (e.g., chokecherry). Krefting and Hansen (1969) used

2,4-D to temporarily reduce hazel populations and change shrub species composition (e.g., in favour of preferred browse species). Tappeiner (1979) achieved between 84 and 100 % mortality of beaked hazel clones by applying 2,4-D at a rate of 1.12 kg/ha.

While there are many studies evaluating the effects of herbivory on plant communities across North America, the specific response of beaked hazel to herbivory is poorly documented. In some cases, heavy ungulate herbivory may cause abrupt, non-linear shifts towards the development of woody plant communities where grasslands formerly dominated (Archer et al. 1988). Other studies show that intense herbivory can be used to reduce shrub populations and restore grasslands (Field and Ross 1976). In EINP, succession has been modified by high ungulate populations (Shultz and Bentz 1992; Polster and Watson 1979). More specifically, heavy browsing has resulted in a shorter, less dense shrub layer that lacks preferred browse species such as chokecherry (*Prunus virginiana* L.) and saskatoon (*Amelanchier alnifolia* Nutt.), and has fewer aspen suckers (Bork et al. 1997b). The proportion of beaked hazel in EINP has increased since 1990, and now contributes up to 62% of available browse and 75% of utilized browse within the Park (Stromsmoe 1994; Blyth et al. 1993).

2.4 Plains Rough Fescue Ecology

Plains rough fescue (*Festuca hallii* (Vasey) Piper) is a cool season bunchgrass most frequently found on black soils in the Mixed Prairie and Aspen Parkland ecoregions of Canada (Trottier 1986; Harms 1985; Bailey and Anderson 1978; Coupland and Brayshaw 1953). Although rough fescue was historically an abundant plant species in central Alberta, much of its range has been converted into cropland due to the area's high

productivity (Willms et al. 1996; Trottier 1986; Moss and Campbell 1947). Plains rough fescue now persists only where conditions prevent cultivation (e.g., areas with unsuitable soils). Trottier (1986) estimated that only 20 000 km^2 of plains rough fescue dominated grassland remains in Canada, of which 90% has been modified by livestock grazing and haying.

There has been some debate on the taxonomy and nomenclature of rough fescues. Pavlick and Looman (1984) differentiated between three rough fescue species: plains rough fescue, foothills rough fescue (*Festuca campestris*), and arctic rough fescue (*Festuca altaica*). Aiken and Lefkovitch (1984) suggest that the spatial distribution of foothills rough fescue indicates that it may be a hybrid of *Festuca hallii* and *Festuca altaica*. *F. campestris* (previously included, along with *Festuca hallii*, as *Festuca scabrella* Torr.) is found primarily in the elevational transition zone from Mixed Prairie to Montane forest in southwestern Alberta (Moss and Campbell 1947).

Festuca hallii is characterized by a palisade of marcescent basal leaf sheaths, deciduous outer leaf blades, densely scabrous leaves, and lemma awns greater than 1 mm in length (Pavlick and Looman 1984). In comparison to *Festuca campestris*, *Festuca hallii* is relatively short, has narrower leaf blades, and usually has short creeping rhizomes. *F. hallii* clumps range from 7 to 10 cm in diameter, with as many as 10 culms standing erect or at an angle of 70 to 80° from the horizontal. Leaves are always tightly folded, and panicles erect.

Several studies have found that both plains and foothills rough fescue initiate growth early in the spring, soon after snow-melt (Willms et al. 1996; Romo et al. 1991; Bailey and Anderson 1978). In fact, Willms et al. (1996) observed that 73% of foothills

rough fescue production occurred in spring, with growth complete by the end of June. Germination of plains rough fescue seed was not limited by temperature, but did depend on moisture availability (Romo et al. 1991). Rough fescue production was less dependent on precipitation during the growing season than other grassland communities, particularly those arising from heavy grazing (e.g., *Danothonia parryi* Scribn. – *Poa pratensis* L.) (Willms et al. 1996).

Fire is an important factor affecting the growth of plains rough fescue (Sinton-Gerling et al. 1995). The effects of fire have been variable, though most studies concur that fescue grasslands are well-adapted to single burns (Sinton-Gerling et al. 1995; Bailey and Anderson 1978). The timing of fire also appears to influence fescue response. Sinton-Gerling et al. (1995) suggested that although burning during any season is tolerated, spring burns have the greatest benefit by increasing tillering and standing crop. In contrast, Bailey and Anderson (1978) found late spring burns were more detrimental to plains rough fescue than fall burns, and reduced canopy cover for up to three years post-burn. Redmann et al. (1993) found that both spring and fall burns delayed grass growth for one full growing season post-burn, but increased the nitrogen content of plains rough fescue.

Grazing is another major factor that greatly affects plains rough fescue production. Foothills rough fescue maintains approximately 76% of its standing crop through winter, making it an excellent dormant season forage (Willms et al. 1996). Plains rough fescue maintains a crude protein level greater than 8.5% throughout most of the growing season, and 6.5% into the dormant season (Horton 1991). The high productivity of this bunchgrass in early spring makes it very susceptible to grazing during

the growing season (Horton 1991; Willms et al. 1985). While light stocking rates did not alter range condition, moderate to heavy stocking rates reduced the basal area of foothills rough fescue (*Festuca scabrella*) and reduced range condition ratings (Willms et al. 1985). Sustained heavy stocking rates have been found to eliminate plains rough fescue (Trottier 1986). Heavy grazing can also reduce soil organic matter, moisture, litter and mulch, and increase soil pH and temperature, indicating that soil under rough fescue can be transformed to that of a drier micro-climate (Naeth and Chanasyk 1995; Naeth et al. 1991a, 1991b; Johnston et al. 1971). In addition, heavy grazing pressure may eliminate rough fescue from the seedbank (Willms and Quinton 1995), potentially accounting for the poor recovery after a reduction in grazing pressure (Willoughby 1997).

Protection from herbivory may increase rough fescue, provided it has not been completely eliminated. McLean and Tisdale (1972) observed that foothills rough fescue recovery on a poor condition site was slow for the first decade, but improved as soon as fair condition was achieved. The general consensus is that rough fescue needs between 20 and 40 years to recover from overgrazing (McLean and Tisdale 1972; Willms et al. 1985; Trottier 1986). However, a study conducted in Riding Mountain National Park, Manitoba, indicated that plains rough fescue is unlikely to re-establish after extirpation *unless* rehabilitative measures such as burning, seeding, and ungulate reductions are under-taken (Trottier 1986).

2.5   Rangeland Reference Areas

Rangeland reference areas typify relatively undisturbed conditions of range growth, and other conditions that have unique characteristics of scientific interest (Allen 1986).

Rangeland reference areas are often established on sites that are susceptible to heavy grazing and browsing by livestock or wildlife, or anywhere the possibility of overgrazing may be a concern. For example, the Alberta Forest Service has a network of 45 reference areas within the Forest Reserve that are used to track the cumulative effects of livestock grazing (Willoughby 1998; Willoughby and Weerstra 1997). Similar programs exist within the Public Lands Branches of Alberta (Downing and Karpuk 1992) and British Columbia (Gayton 1998), and other grazing administrations throughout western Canada and the United States.

There are generally four categories of rangeland reference areas. These include research natural areas, exclosures, managed range study areas, and other reference areas (Allen 1986; Laycock 1975). Research natural areas are large baseline areas that are representative of original or climax vegetation, and receive non-destructive management. Exclosures are smaller areas set aside and protected from animal use by a barrier such as a fence. Managed range study areas are grazed areas that illustrate excellent range condition or a specific type of livestock management. Other reference areas include educational areas, botanical or geological areas, recreational areas, and endangered species preserves.

As a national park, EINP in its entirety would fit into the research natural area division provided it is in good range condition. While EINP remains a very productive system, vegetation within the Park has been heavily over-utilized by elk, moose and bison, and significant vegetational changes have occurred (Bork et al. 1997a). Range deterioration in EINP may be attributable to ungulate stocking rates within the Park over

the last 80[+] years. Despite this concern, limited work was done to estimate range

condition and trend prior to 1970.

Previous vegetation monitoring within EINP occurred as early as the 1970s and

included browse surveys, exotic plant surveys, and range production assessment, as well

as ecological land classifications (Cool 1999; Osko 1995, 1993; Blyth et al. 1993;

Stromsmoe 1992; Hardy et al. 1986; Polster and Watson 1979). In the early 1990s range

condition assessment and overstory classifications were implemented throughout the Park

(Cool 1999; Blyth et al. 1993; Schultz and Bentz 1992). More recently, in 1997,

permanent sample plots (PSPs) were established to monitor overstory, understory, and

environmental characteristics of upland rangelands within the Park (Cool 1999; Equus

Consulting Inc. 1997). While Park management has become increasingly concerned with

habitat monitoring, few of the previous methods have facilitated a comparison between

grazed and ungrazed plant communities. Exclosed reference areas offer a tool for

assessing long-term rangeland trend and vegetation recovery from ungulate herbivory

within the Park, and will complement the PSP program.

Exclosures are any experimental areas protected from the activities of a particular

type of herbivore by a barrier (Daubenmire 1940). There are two general types of

exclosures. The first is a single exclosure that excludes one of three animal groups:

livestock, livestock and big game, or all mammals. The second exclosure type consists of

multiple exclosures where one excludes big game, and another excludes livestock, game,

and/or rodents.

Allen (1986) and Laycock (1975) list several reasons for the preservation of natural

areas in the form of rangeland reference areas. Rangeland reference areas may serve as

educational tools, genetic banks, and act as a mechanism to assess the condition of representative plant communities. Some rangeland reference areas represent unhindered biological and physical processes and become a baseline with which to compare man's influence. In some cases, rangeland reference areas are the only remaining sources of relatively undisturbed vegetation available for specific range sites.

An important benefit of exclosures is that they may be used to assess range condition and trend under various disturbances (Laycock 1975, Beetle 1974). Traditionally, if plant species composition differed in and outside the exclosure, the plant species abundant inside were named decreasers, while the plant species favoured outside were termed increasers, and relative plant species composition was accepted as an indication of range condition (Beetle 1974). Exclosures are also an important tool when evaluating vegetation recovery from herbivory, as they facilitate observation of individual plant species response, as well as changes in plant community diversity, productivity, vegetation structure, and soil characteristics following the removal of herbivory. Thus, exclosures provide a potential tool to assess vegetation resilience to herbivory.

Finally, exclosures provide an opportunity to determine the identity of those specific plant species that would increase in abundance on various rangeland sites following the removal of herbivory, either by recovering in vigor and stature, or by re-establishing over time. Re-establishment may be from either seed sources within the soil seed bank, or by immigration from outside areas.

Disadvantages of an exclosure program include the fact that interpretations based on exclosure data require awareness that protected vegetation sets a false standard which increases in artificiality over time (Beetle 1974). Most rangelands have evolved under

the effects of herbivory (Holechek et al. 1998; Savory 1988) and the removal of herbivory means that the area inside the exclosure is not in a 'natural' state. Thus, depending on the research objectives, it may be equally valuable to evaluate range utilization by various ungulate species or combinations thereof (Cook and Stubbendieck 1986).

In addition, site characteristics such as soil conditions, topography, and aspect greatly influence potential vegetation development (Holechek et al. 1998). Therefore, not all vegetation changes inside exclosures can be attributed to reduced grazing and browsing (Brand and Goetz 1986).

Other disadvantages of exclosures are fence effects, excessive mulch and litter accumulations, increased rodent populations and the loss of productivity and biodiversity with the removal of herbivory (Laycock 1975). Fence effects include snow trapping and changes in moisture distribution. This becomes more important as the size of the exclosure decreases and the aridity of the area increases. More snow may collect when fences are close together. Fences also attract birds that may distribute seeds along the fence-line, thus facilitating changes in plant species composition. Increases in rodent populations may also be attributable to exclosures, as they protect areas from ungulates and increase vegetation and litter cover, and therefore, the quality of small mammal habitat.

The elimination of ungulate herbivory has been shown to cause vegetation stagnation and decreased biodiversity and productivity (Willoughby 1992). Exclosures allow for the accumulation of mulch and litter, reducing the number of shoots per unit area and the number of flower stalks (Wan and Sosebee 2000; Laycock 1975).

The size and distribution of exclosures may also limit their usefulness on a coarser scale. Small, isolated exclosures are not representative of larger areas and are difficult to extrapolate to the larger areas at which management occurs. This is due to variation in site characteristics (e.g., soil, topography, microclimate, effective moisture regime, etc.) (Bork et al. 1998). The effective distribution of exclosures throughout an area (and stratification by topography) helps to counteract this problem.

2.6   Previous Management in EINP

Early European records show that bison herds near EINP were used to sustain large Plains Indian populations prior to European settlement (Blyth 1995). Fire was used by aboriginals in the Beaver Hills to burn forest and increase grassland available to game species (Blyth 1995). Around 1795 the area was settled by fur traders and by 1815 almost all beaver had disappeared. By the late 1860's, bison were nearly eliminated and other ungulates were scarce. The Plains Indians were restricted to reserves, and the incidence of fire reduced. Reduction of fire and native ungulate herbivory led to increased aspen succession throughout the Beaver Hills.

In 1895, a large wildfire destroyed what forests had become established and several years later in 1899, the area was set aside as the Cooking Lake Forest Reserve. In 1906, Elk Park was established and 42 square kilometres fenced as a native ungulate sanctuary. The park was christened Elk Island in 1913, and designated an "animal park", with management strategies such as hay cutting and eradicating predators acceptable. Inventories of ungulate populations were carefully conducted.

By 1917, native range within the Park was considered overgrazed by moose and elk (Coxford 1917). Elk Island was expanded in 1923 to include another 94 km^2, but in 1928 the ungulate numbers were still perceived as excessive and reduced by slaughter. Another slaughter occurred in 1935, but bison and elk populations remained above 2000 (Blyth 1995), resulting in significant winter mortality and public criticism.

Elk Island became a National Park in 1930, but this had little impact on management strategies. Large ungulate populations continued to exist into the 1940's and 50's, and control measures included annual slaughters and live-trapping. In 1949 EINP was again expanded, with the new area used as a quarantine for brucellosis eradication. During this period introduced grass species were planted to increase the hay crop available for winter feeding. Ungulate numbers were reduced by 45% in 1959, allowing for increased aspen succession (Blyth 1995).

The present plains bison herd originated from a herd pastured there temporarily in 1907. When these bison were relocated in 1909, some evaded capture and the remaining herd expanded. Wood bison were introduced in 1965 to the Isolation area south of Highway 16 and have been maintained geographically separate from the plains bison herd ever since.

Currently, lack of effective predators and the presence of a perimeter fence have placed a large demand on forage resources within the Park (Bishoff 1981). Bison still receive hay supplements during winter. As a result, bison populations have not experienced the rapid decline that might be expected when numbers reach ecological carrying capacity. Bison and elk numbers, and disease free status are maintained by

annual round-ups, translocation, and sales to private ranches. Additional fences and facilities (e.g., corrals) have been constructed to facilitate handling.

As a result of an ecosystem management workshop in August 1997, present management is committed to the preservation and restoration of natural ecological processes in order to maintain the temporal and spatial characteristics of a native Aspen Parkland and Lower Boreal Mixedwood grazing system (Cool 1999; Equus Consulting Inc. 1997; Blyth 1995). Specific management objectives include re-introduction of fire as a natural process, improved habitat monitoring, and reduction of ungulate populations. To facilitate biological monitoring and management, the Park has been conceptually divided into three land management units (LMU) (Equus Consulting Inc. 1997). The south LMU is located south of Highway 16, and is physically separate from the Main Park (Figure 2.1). The central and north LMUs are north of Highway 16. Within each LMU, four long-term biomonitoring plots (LTBP) (0.5 by 2 km) have been established for monitoring Elk Island's natural resources (Cool 1999).

Figure 2.1: Map of Elk Island National Park and exclosure locations.

2.7   Native Ungulates in EINP

The major native ungulates found in EINP are bison, elk, and moose. Bison are divided into two herds: the Plains bison (*Bison bison*) north of Highway 16 and the Wood bison (*Bison athabascae*) in the Isolation unit to the south. Elk (*Cervus canadensis*) and moose (*Alces alces*) also wander freely throughout EINP, but may be limited by interspecific competition for forage (Blyth 1995). Whitetail (*Odocoileus virginianus*) and Mule (*Odocoileus hemionus*) deer are also common, but the 8 foot perimeter fence is not considered a deterrent to deer movement. Overall, deer contribute relatively little to forage demand within the Park (Table 2.1).

Table 2.1: Approximate ungulate populations in the Main Park and Isolation Area of EINP for the period 1910 to 1999 [values compiled from Blyth (1995) and Parks Canada (1999)].

Ungulate species	1910	1920	1930	1940	1950	1960	1970	1980	1990	1999
Main Park *(13600 ha)*										
Moose	19	70	400	113	272	83	280	380	231	250
Elk	30	200	467	473	800	154	350	500	872	1450
Plains Bison	45	200	716	995	1350	750	831	421	444	638
Mule Deer	30	150	200	27	150	0	-	-	-	-
Whitetail Deer	-	-	-	-	1	90	74	120	201	150
Isolation Area *(5800 ha)*										
Moose	-	-	-	-	-	80	225	100	77	90
Elk	-	-	-	-	-	90	25	75	320	420
Plains Bison	-	-	-	-	75	236	0	-	-	-
Wood Bison	-	-	-	-	-	-	32	110	232	405
Whitetail Deer	-	-	-	-	-	155	265	130	65	60
Total *(19400 ha)*	124	620	1783	1608	2648	1638	2082	1836	2442	3463*

* Equivalent to a continuous stocking rate of 2.0 AUM/ha throughout the Park.

Together, bison, elk and moose impose a large demand on available forage within the Park. In the 1970's, Telfer and Scotter (1975) postulated maximum ungulate densities for EINP to be 33 bison, 13 elk, and 7 moose per square mile. These values were derived under the assumption that bison would receive hay supplements during winter, so it is probable that current recommended year-long stocking densities should be significantly lower than this. Even though EINP is a highly productive ecosystem

capable of rapid vegetation succession (Blyth 1995), the Park may not be able to sustain current ungulate densities in the long-term.

Major predators historically found in the ecosystem represented by the Park include grizzly bear (*Ursus horribilis*), wolf (*Canis lupus*), cougar (*Felis concolor*), and coyote (*Canis latrans*) (Blyth 1995). Today, with the imposition of the perimeter fence, and the local extirpation of most carnivores, only coyotes remain as predators. Despite being an efficient predator of smaller prey species like the snowshoe hare (*Lepus americanus*), coyotes are not an adequate control measure for the abundant large ungulates, except perhaps deer.

2.8   Herbivory in EINP

One of the most influential disturbances on vegetation in Elk Island National Park is native ungulate herbivory. High ungulate populations over many decades have over-utilized vegetation within EINP, inhibiting grassland succession to aspen forest while changing the species composition of the herb and browse communities (Bork et al. 1997a, 1997b).

In EINP, not all sites are utilized with equal grazing pressure. Relatively greater use occurs on south-facing slopes, particularly in spring. These areas have a greater abundance of grazing tolerant, introduced rhizomatous species (Bork et al. 1997b). These species maintain rapid growth when intensively grazed, and are therefore most likely to respond rapidly to protection from grazing (Bedunah and Sosebee 1995).

Another factor influencing the condition of EINP rangelands is the fact that the Park is fenced and ungulates are not allowed to migrate to and from adjacent land areas.

This affects the temporal pattern of vegetation use by large herbivores. Bison traditionally wintered in the aspen parklands, and summered on the prairie (Morgan 1980). This seasonal migration gave the grazing-sensitive native forage species, particularly the bunchgrasses, time to recuperate during the following summer. Also, the nomadic grazing habits of bison meant that once a spot was grazed, it was probably ungrazed for several years, allowing it to fully recover. Coughenour (1991) observed that the spatial component is central to domestic and native ungulate systems and nomadism seems sustainable. Today, with the modern dissection of land by fences, roads, cities and farms, historical grazing patterns are virtually impossible to replicate.

The construction of small, ungulate-proof exclosures within EINP will allow a direct comparison to be made between rangeland exposed to continuous intense native ungulate grazing/browsing and areas protected from ungulate herbivory. In doing so, vegetation recovery can be monitored through time, including species composition, diversity, productivity, and structure, along with the associated soil characteristics (litter, soil cover, etc.), all of which are important for maintaining "rangeland health" (NRC 1994).

In addition to assessing the current (short-term) impacts of herbivory, exclosures will serve as a critical tool for determining what rangeland vegetation *could* succeed to following a reduction in ungulate stocking rates within the Park. This is particularly important because, on the heavily grazed south-facing slopes (e.g., grazing lawns), reduced herbivory may not facilitate a return to "climax" Aspen Parkland vegetation, but rather some other vegetation dominated by introduced species. Willoughby (1997) found that after 40 to 50 years of livestock exclusion, exclosures in southwestern Alberta were

still dominated by introduced species, suggesting that heavy grazing reduces plant community/species resilience, and inherent thresholds may have been crossed.

Furthermore, given that the removal of herbivory may decrease the diversity and productivity of rangeland (Fahnestock and Knapp 1994), exclosures can be used to determine what the removal of grazing would do to vegetation diversity within EINP, in both the short and long-term. An exclosure program can also document the anticipated effects of any major changes in ungulate management (e.g., reductions in animal numbers) within several 'test' areas, prior to their actual implementation in the Park. In turn, this will provide a better understanding of the role native ungulate herbivory plays in maintaining and/or limiting native plant species biodiversity.

Exclosures will also be useful in the monitoring of individual plant species responses in EINP. For example, aspen regeneration in the Park has been largely suppressed in the past by intensive browsing (Bork et al. 1997b). Release from browsing will likely increase tree recruitment as several studies have found that exclusion of grazing was needed to allow aspen to sucker and grow (Kay and Bartos 2000; Harniss and Bartos 1990; Bailey et al. 1990; Trottier and Rohlf 1982). Harniss and Bartos (1990) also noted that if no livestock grazed the area, but wild ungulates had access, aspen return was spotty and less vigorous in appearance than within completely protected areas. Beaked hazel (*Corylus cornuta*) also provides a large proportion of the available browse during winter in EINP. This species, along with other shrubs, has adapted to years of intense browsing by increasing stem density (Bork et al. 1997b). The removal of browsing may change the growth form and/or productivity of these important species.

The construction of burn-tolerant exclosures (e.g., all metal materials) in EINP will allow differentiation between the combined effects of fire and herbivory on vegetation versus fire alone by allowing areas inside the exclosures to burn along with the surrounding vegetation. The exclosures in EINP will be used as tools to assess the potential maximum rate of vegetation recovery if ungulate stocking rates were reduced.

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CHAPTER 3: Vegetation Resilience Following Ungulate Removal in Elk Island National Park, Alberta.

3.1 Introduction

Elk Island National Park (EINP) is managed to conserve part of the Aspen Parkland and Lower Boreal Mixedwood ecoregions of Canada. As a national park, it has been set aside to preserve the ecological integrity and biodiversity of the region for the education and enjoyment of future generations (Parks Canada 1988). Management in Elk Island National Park (EINP) has historically focused on key ungulate species, but is becoming increasingly concerned with vegetation, habitat, and ecosystem processes (Equus Consulting Inc. 1997).

Herbivory is a major disturbance in EINP and heavily impacts plant community composition, diversity, structure and production (Bork et al. 1997a, 1997b). In general, intensive year-long ungulate herbivory has reduced the height of the forest understory, resulting in a shift within plant communities towards shorter herbs and browsing tolerant shrubs (e.g., *Corylus cornuta* Marsh) (Bork et al. 1997a). On open grasslands, native herbs have been largely replaced by invasive, exotic herbaceous species (e.g., *Poa pratensis* L., *Taraxacum officinale* Weber, *Plantago major* L.) (Bork et al. 1997a). These ecological changes are the cumulative result of the Park's small size, fenced perimeter, and high ungulate populations over the last 80 years (Parks Canada 1999). As native ungulate populations continue to increase, so does the demand for forage from rangelands, making it even more important to understand the impacts of ungulates on vegetation within the Park. The effects of herbivory on primary productivity, plant community composition, and structure are important factors determining the long-term

sustainability of ecosystems (Lecain et al. 2000). The current challenge for EINP resource managers is to effectively manage rangelands for providing habitat and forage to wildlife, while preserving floral diversity (both composition and structure).

While several studies have documented the changes in floral diversity, structure and production in EINP associated with high ungulate populations (Bork et al. 1997a, 1997b; Milner 1977), the potential for recovery of these rangelands following a reduction in herbivory has not been assessed. Current models of vegetation dynamics indicate that rangelands are susceptible to complex non-linear responses, including the presence of multiple stable states and thresholds (Laycock 1991; Friedal 1991; Westoby et al.1989). Bork et al. (1997a) proposed a model of vegetation dynamics for uplands within EINP, with fire, herbivory and forest succession as key driving factors. Intensive herbivory, particularly on open grasslands, increases exotic species, which is theorized to represent a shift across an ecological threshold, with recovery unlikely to occur with the removal or reduction of herbivores (Bork et al. 1997a). In other regions of Alberta and western Canada, protection from grazing on rangelands invaded by exotic species has failed to facilitate the recovery of native species (Willoughby 1997; Trottier 1986).

As a result of a workshop held in 1997, the Park was conceptually divided into three land management units (LMU) to facilitate biological monitoring and management (Equus Consulting Inc. 1997). In order to test the resilience of plant communities within the Park following the removal of intense herbivory, an experiment using permanent exclosures was initiated in 1998 to complement the bio-monitoring program. The results discussed here represent the initial (2 year) vegetation responses.

It was hypothesized that if rangelands were highly resilient to ungulate herbivory, plant communities protected from herbivory would be structurally and compositionally more diverse within two years, and produce more above-ground phytomass than adjacent areas exposed to herbivory. In contrast, non-resilient communities would be unable to recover, with negligible changes in species composition and structure. Specific hypotheses include:

H_{A1}: Plant species cover, richness and community diversity, particularly of native species, will increase within exclosures over the two year study period and be greater than similar areas outside exclosures.

H_{A2}: Vegetation will increase in height and shift towards taller species within the exclosures during the two years of the study.

H_{A3}: Herb standing crop and shrub current annual growth will be greater within exclosed plant communities.

3.2 Study Area

EINP (53°37'N, 112°58'W) is located within the Beaverhills – Cooking Lake Moraine, approximately 37 km east of Edmonton, Alberta. It encompasses 194 km^2 of ridged to hummocky terrain with slopes between approximately 0 and 20%. Elevations vary from 710 to 760 m ASL.

Bork et al. (1997a) documented several major plant community types in EINP, and found strong topographic and disturbance (both fire and herbivory) effects on vegetation. Roughly 80% of the Park is dominated by trembling aspen (*Populus tremuloides* Michx.) forest, which occupies the majority of upland range sites. Beaked hazel (*Corylus cornuta* Marsh) and marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) dominate the shrub and herb layers of aspen stands. Vegetation on drier sites within the Park (e.g., south-facing slopes) is largely composed of introduced species

including Kentucky bluegrass (*Poa pratensis*) and dandelion (*Taraxacum officinale*), and some shrubs (e.g., *Symphoricarpos occidentalis* Hook.).

Soils on upland sites are well to moderately well-drained Orthic Grey Luvisols, while Dark Grey Luvisols are found on less densely treed, more open areas, and Gleyed Grey Luvisols occupy lower slopes (Crown 1977). Soil textures vary from loam to silty loam or loamy sand.

Located in the cool continental, sub-humid climatic region, EINP receives about 450 mm of precipitation annually, with 75% falling as summer rain (Environment Canada 1993). Temperatures vary from -40°C in winter to 32°C in summer.

Elk Island is the only fenced national park in Canada. Substantial ungulate populations are found in the Park, and place great demand on the vegetation all year, as animal migration is restricted by the 2.2 m perimeter fence. In 1999, roughly 640 plains bison (*Bison bison*), 400 wood bison (*Bison athabascae*), 340 moose (*Alces alces*), 1850 elk (*Cervus elaphus*), and fluctuating whitetail and mule deer populations (*Odocoileus virginianus* and *O. hemionus*) were supported by the habitat in EINP (Parks Canada 1999). These year-long stocking densities (Table 3.1) are among the greatest in North America.

Current bio-monitoring programs within the Park occur in the LMUs established in 1997 (Equus Consulting Inc. 1997). The south LMU is located south of Highway 16, and is physically separate from the Main Park. The central and northern LMUs are north of Highway 16. Within each LMU, four long-term bio-monitoring plots (LTBP) (0.5 by 2 km) have been established for monitoring Elk Island's natural resources (Cool 1999).

3.3 Exclosure Establishment

Six ungulate exclosures were established within EINP during the winter of 1998-99 creating two treatments (grazed/browsed versus ungrazed/unbrowsed) at each location. Exclosures were stratified throughout the Park, with two in each LMU. Furthermore, each exclosure was located within a LTBP to complement other bio-monitoring programs. Each exclosure was 20 by 50 m, of all metal construction to withstand burning, and 2.2 m high. At each exclosure, paired areas inside and outside were similar in ecosite conditions (e.g., slope and aspect), as well as initial vegetation composition and structure (Table 3.2).

At each exclosure, two vegetation types on unique ecosites occurred both inside and outside. These included forest dominated by aspen and balsam poplar (*Populus balsamifera* L.) with an understory of beaked hazel and various herbs on north slopes and crest topographic positions, as well as grassland dominated by Kentucky bluegrass, marsh reedgrass, and a shrub layer varying from sparse to nearly continuous on south-facing slopes. This experimental design resulted in 24 plant communities, four at each exclosure, with two forested and two grassland, one of each of which was grazed/browsed.

3.4 Field Sampling

3.4.1 Ecosite Characteristics

Within each vegetation type, ecosite data was collected on slope gradient, aspect, precipitation and soils (Table 3.2). Average slope was measured using a clinometer,

while aspect was determined using a compass from the centre of the plant community. Precipitation was collected in rain gauges at each of the six exclosures during the summers of 1999 and 2000 (May to September). Six soil cores (30 cm deep and 2 cm diameter) were collected from random locations within each plant community at the end of October 2000. Cores were divided into two depth classes: 0 to 15 cm, and 15 to 30 cm, then composited within a depth class to yield 2 samples per plant community. All soils were air-dried and sent to Norwest Labs (Edmonton, Alberta) for chemical analysis. Soil texture analysis was performed using the hydrometer method (McKeague 1978).

3.4.2 Understory Species Composition & Structure

Species cover was sampled in each plant community during peak vegetative growth (e.g., July) of 1999 and 2000, the first and second years following exclosure construction. Two, 15 m transects were randomly located in each plant community, grassland and forest, grazed and ungrazed, and are mapped in Appendix 2. On each transect, 8 nested quadrats were sub-sampled (at the 0 metre mark and every 2 meters thereafter) for species composition and community structure, with sub-samples from both transects pooled (n = 16) to obtain a mean value for the plant community, which was then used in subsequent analysis. The total sample size was determined by collecting pilot data on forest and grassland sites as illustrated in Appendix 1. Nested quadrats at each sample point included a 1 m^2 quadrat and a 0.4 by 0.5 m quadrat. Quadrats were consistently placed on the north (up-slope) side of transects in grassland communities and the south side of transects within forest communities. Shrub density and cover by species, along with maximum shrub and herb height were measured in the 1 m^2 quadrat,

while herbaceous cover was estimated in the smaller quadrat. All cover values were estimated to the nearest percent using ocular estimation (Daubenmire 1959). Shrubs were defined as woody species less than 2.5 m tall. Species cover estimates were used to calculate both native and exotic species richness and Shannon diversity indices for each of the 24 plant communities examined (Kent and Coker 1992; Cook and Stubbendieck 1986).

3.4.3 Herb Standing Crop & Shrub Current Annual Growth

Standing crop (SC) of herbs and current annual growth (CAG) of shrubs was collected in August of each year. A 0.5 by 0.5 m quadrat was sampled at the 5 and 11 m positions on each transect (n = 4/plant community), and all clippings separated into three growth forms: grasses, forbs and shrubs. SC and CAG was oven dried at 50°C for 48 hours, and weighed. In 1999, the first year following ungulate exclusion, utilization was calculated for grassland communities by contrasting grazed and ungrazed plant community herb standing crop. In the second year of the study (2000), additional sampling was done by randomly placing two range cages on the grazed grassland plant community at each exclosure, and clipping using the same methods described above. The latter information was used to compare maximum production after one and two years of rest, and to determine the relative utilization of vegetation in 2000 on grazed grasslands.

3.4.4 Vegetation Overstory Parameters

The tree overstory was sampled in detail. Diameter at breast height (DBH) was measured at 1.3 m for all trees in two belted transects (2 by 15 m) centred on each species

composition transect (see section 3.4.2). Tree canopy cover (where applicable) was also estimated along each transect using the line intercept method (Bonham 1989). Tree height was estimated using a clinometre for ten trees randomly selected from each forested site, and all trees present on grassland sites. Tree density was counted in 20 by 20 m plots, and included all trees taller than 2.5 m. Tree regeneration (< 2.5 m) was measured using density counts in shrub density quadrats.

3.4.5 Exotic Species Removal

Two additional transects were located in the protected grassland communities at each of four exclosures to evaluate the short-term response of native plants to the removal of competition from invasive/exotic plants. Only exclosures with grassland sites dominated by Kentucky bluegrass were used (n = 4) for two reasons: (1) Kentucky bluegrass is an exotic species and has been associated with the suppression of native species recovery (Willoughby 1997; Trottier 1986), and (2) the remaining grassland plant communities were dominated by marsh reedgrass, which is a relatively unpalatable native species (Gainer 1987; Stout and Brooke 1985) and may not experience the heavy summer grazing levels found on Kentucky bluegrass dominated sites.

On each ungrazed grassland, ten plastic pails (30 cm diameter) were cut to form cylinders approximately 25 cm long, and placed at regular intervals along two transects (5 pails per transect). Pails, or exotic species removal (ESR) plots, were carefully inserted 20 cm into the ground using pre-cut slots in May of 1999 with minimal vegetation disturbance. Pails were used to eliminate root competition and encroachment from outside vegetation. Plants inside the ESR plots were immediately treated with

glyphosphate, a non-selective, non-residual herbicide, and monitored throughout the growing seasons of 1999 and 2000. All exotic species were subsequently pulled from the plots as they emerged. Native species cover inside ESR plots, and in a corresponding untreated paired plot adjacent to each ESR plot, was estimated in August of 1999 and 2000. Native species plant density was also assessed in 2000.

3.5 Data Analysis

Species cover data was summarized by functional groups for analysis, and included native plants, exotic plants, legumes, grasses, forbs, and shrubs to determine the effects of removing herbivory on these important functional groups (Hector et al. 1999; Tracy and McNaughton 1997). All data were checked for normality and homogeneity prior to statistical analysis. Data found to be non-normal or heterogenous using the Shapiro-Wilkes statistic were transformed (Sokal and Rohlf 1995). Species richness and DBH data required reciprocal transformations. Square-root transformations were used on grass and forb range cage SC data, and shrub CAG, as well as forb density in the vegetation regrowth plots. Log transformations were used for shrub cover and diversity.

Plant communities (N = 24) were considered the experimental unit in this investigation, with all data analyzed using a split-block design. Vegetation communities were treated as split-plots within each grazing treatment, with six blocked replicates (exclosures) overall. Tests for the effects of exclosure location (e.g., block), grazing treatment, vegetation type (grassland vs. forest), and interactions of main treatments were conducted on all variables with ANOVA using General Linear Model (GLM) Procedures (SAS 1991). An alpha level of $p<0.10$ was used to determine statistical significance.

Post-hoc mean comparisons were conducted on all significant variables using Tukey's test ($p<0.10$). Grazing and vegetation type were analyzed as fixed effects, and exclosure location treated as random.

3.6 Results & Discussion

3.6.1 Ecosite Characteristics

All soil properties tested, except ammonium, varied among exclosure locations ($p<0.10$). Of the six locations, Shirley generally had the greatest soil nutrient content. Ranger, Boreal, Astotin, and Tawayik exclosure locations had relatively similar soil properties, while soils at Bailey contained relatively low amounts of nutrients. Variation in soil properties among locations is likely due to differences in ecosite characteristics and management regime (Table 3.2). For example, the recent burn history of the Shirley area (e.g., spring burns in 1989, 1991, 1993) may have elevated calcium, magnesium, organic matter, potassium and sulphate at this location by increasing nutrient cycling (e.g., combustion, or mortality of plants and subsequent root decomposition) (Holechek et al. 1998; Bedunah and Sosebee 1995). In addition, increased clay content of soils at the Shirley exclosure location (Table 3.2) may result in greater nutrient binding capacity of those soils. In contrast, soils at Bailey were very sandy (Table 3.2), likely accounting for the lower pH, electrical conductivity and calcium, relative to other sites.

No differences between grazing treatments were found (Table 3.3), likely due to the long time period (> 2 years) typically necessary for soil genesis to occur. As might be

expected, vegetation type was related to select soil properties (Table 3.3). Forested areas were lower in pH, but greater in potassium and phosphorous than grasslands.

3.6.2 Vegetation Overstory Parameters

Tree canopy cover, density and regeneration varied significantly among exclosure locations ($p<0.05$), but were similar between grazing treatments (Table 3.4). In addition, with the exception of tree regeneration, all overstory parameters varied as expected with vegetation type ($p<0.01$).

Of the six locations, the Boreal and Tawayik exclosures had the greatest tree density and canopy cover, as well as relatively taller trees, all indicative of more closed aspen forest (Table 3.4). However, trees at Tawayik also had the lowest DBH measurements, indicating that forest communities at this exclosure location may be relatively young. In contrast, the Astotin exclosure location was more open and less dense (Table 3.4). DBH measurements indicated that trees at this location may be the oldest observed in the study. Visual reconnaissance suggested it was a decadent aspen stand, with few trees and many dead snags contributing to an open canopy. The remaining three locations (Ranger, Shirley, and Bailey) were relatively similar in tree canopy cover, density and height (Table 3.4), and are probably mid-seral aspen forests.

The lack of response to grazing treatment was expected, as changes to overstory parameters resulting from the removal of disturbance should take many years (e.g., 10 to 20 years) to develop (Harniss and Bartos 1990). However, one variable that was expected to respond quickly to the removal of grazing was tree regeneration, which varied among exclosures, but did not respond to grazing treatment or vegetation type in

the first two years of protection (Table 3.4). The overall low levels of regeneration found support other studies that have indicated prolonged intense herbivory significantly affects aspen regeneration (Kay and Bartos 2000; Campbell et al. 1994; Hobbs and Huenneke 1992; Bailey et al. 1990; Trottier and Rohlf 1982), but also indicates aspen recovery following the complete removal of herbivory is not immediate. Aspen is a preferred browse species (Renecker and Hudson 1988; Hobbs et al. 1982; Bischoff 1981) and is utilized at high rates in EINP (Blyth et al. 1993), resulting in a decrease in aspen regeneration within the Park over the long-term (Bork et al. 1997b).

3.6.3 Understory Species Composition & Structure

Many of the understory parameters measured varied among exclosure locations and vegetation type. In 1999, exotic species cover and shrub height varied with exclosure location while in 2000, shrub height, exotic species diversity, and exotic and native species richness, as well as litter, shrub, and exotic species cover varied with exclosure location ($p < 0.10$; Tables 3.4, 3.5 and 3.6). Appendix 3 contains a complete list of species found during the study.

Differences in plant species composition and litter cover observed between exclosure locations may be the result of differences in ecosite characteristics, vegetation structure, local grazing regimes, and Park management (e.g., burning). For example, the Astotin and Boreal exclosure locations had low exotic species cover and relatively high amounts of leaf litter (Tables 3.5). Both locations had productive herb and shrub layers (Table 3.7), which contribute considerable phytomass to the litter pool. In addition, herb and shrub height, as well as shrub cover, were greatest at these locations relative to other

locations (Tables 3.4 and 3.5). Plant community structure (e.g., differences in growth forms, especially increased shrub production) likely plays a key role in litter accumulation, which has been found to detrimentally affect exotic species (e.g., Kentucky bluegrass) (Towne and Owensby 1984).

In addition, native species composition may have a major influence on exotic species abundance at the Boreal and Astotin locations. Interspecific competition may directly limit invasion by exotic species. The dominant plant species (marsh reedgrass and beaked hazel) found at these locations (Table 3.6) have both been found to detrimentally affect micro-site colonization by other species due to intense competition for resources such as solar radiation and soil nutrients (Landhausser and Lieffers 1994; Tappeiner 1971).

It is also possible that reduced grazing at these sites may limit opportunities for invasion by exotic species by reducing the amount of light available to prostrate plants (Tracy and Sanderson 2000), particularly given the low palatability of marsh reedgrass (Gainer 1987; Stout and Brooke 1985). Elsewhere, grazing has been found to increase total nitrogen availability (Dormaar and Willms 1998; Dormaar et al. 1990). This, in turn, may lead to increases in nitrogen-loving plants such as grasses and exotic species (Stohlgren et al. 1999; Johnston et al. 1971; Brown 1939), especially Kentucky bluegrass (Jiang and Hull 2000). Although a trend in soil nitrogen was not evident in this short-term study, this may be because only ammonium was assessed in the fall (e.g., October), which may not adequately represent total soil nitrogen, particularly in spring. Herb utilization data among exclosure locations indicated that while Astotin experienced low to moderate grazing pressure, the Boreal exclosure was more heavily utilized (Figure

3.1). However, herb height at both locations (even with high levels of herbivory) may be sufficient to deter invasion by exotic species (Table 3.5).

Plant communities at the Bailey exclosure location had relatively high native species richness and diversity indices (Table 3.5). In contrast, herb and shrub height, as well as litter, exotic species, and shrub cover were among the lowest. One explanation for this is that limited soil nutrients (Table 3.3) and the sandy soil (Table 3.2) at this location may inhibit exotic species invasion and growth. On the other hand, native species cover did not seem to be affected by the poorer physical site conditions (Table 3.5). This may indicate that native plants are better adapted to cope with this type of environmental (e.g., soil) conditions, or conversely, that exotic species respond more positively to grazing only with optimal conditions for plant growth (Milberg et al. 1999).

The Shirley location was characterized by plant communities with herbs and shrubs of moderate height and cover, as well as high litter cover (Tables 3.4, 3.5, and 3.6). Richness, diversity and the abundance of native and exotic species were moderate as well (Tables 3.4, 3.5, and 3.6). Recent burning (spring of 1989, 1991, and 1993) in the Shirley area may have limited exotic species invasion by reducing plant survival and vigour. For example, Kentucky bluegrass is a dominant exotic species found in the Park (Bork et al. 1997a), and has been found to decline with spring burning (Towne and Owensby 1984). Fire may have also altered ungulate utilization patterns in the Shirley area, as burning has resulted in a more open landscape. This may have distributed grazing more uniformly, leading to reduced utilization near this exclosure (Figure 3.1) and increased recovery of native plant species. In addition to burning, other factors such

as abundant litter and the presence of shrubs may contribute to lower levels of exotic species at this location (Weaver and Rowland 1952).

The two remaining exclosure locations were similar in composition and structure. Both the Ranger and Tawayik locations had elevated levels of exotic species and reduced native species richness, diversity and litter, as well as low shrub height and cover (Tables 3.4, 3.5, and 3.6). Historical ungulate herbivory is probably the major influence on plant community composition at these sites. The area around the Ranger exclosure is heavily utilized by ungulates during the growing season (Figure 3.1), and grassland communities at both locations are dominated by Kentucky bluegrass and clover, both of which are indicators of heavy grazing and subsequent changes to soil and ecosite conditions (Kay and Bartos 2000; Tracy and Sanderson 2000; Willoughby 1997; Willms et al. 1985).

As expected, several plant community parameters were also influenced by vegetation type, including shrub and herb height, and litter, exotic, and native species cover (p<0.10; Tables 3.4, 3.5, and 3.6). Most of the forested communities had northern aspects and relatively greater tree canopy cover than grasslands (Tables 3.2 and 3.4). These conditions would result in a more shaded mesic environment relative to open, south-facing grassland communities, and account for the observed differences in species composition and structure. The greater exotic species cover on grasslands confirms the findings of Bork et al. (1997a), who described open areas as short-structured grasslands that were dominated by opportunistic, grazing-resistant invasive species.

The short-term response of understory species compositional and structural characteristics to the removal of herbivory was limited (Tables 3.4, 3.5, and 3.6). Shrub height and cover, and native species richness were the only understory variables that

responded to grazing (p<0.10; Tables 3.4), with all three increasing following protection. These results corroborate the notion that shrub growth is limited by intense herbivory within the Park (Bork et al. 1997b), and are consistent with previous studies conducted in other regions (Kay and Bartos 2000; Bailey et al. 1990; Trottier and Rohlf 1982). The lack of response of exotic and native species cover and diversity, as well as herb height, during the two years of the study, suggests that the short-term resilience of plant communities within the Park is low, likely due to prolonged heavy grazing over the last several decades. Grazing may also limit the growth of some plant species more than others. Other studies have shown that native plant communities exposed to heavy grazing may require more than 30 years to recover, even if grazing is removed (Trottier 1986; McLean and Tisdale 1972; Pegau 1970), due to the competitive nature of exotic plant species (Willoughby 1997; Bookman 1983) and potential soil degradation during the interim (Dormaar and Willms 2000). Therefore, changes in species composition and structure following the removal of herbivory in EINP may only be attainable in the long-term, and would not be documented by short-term monitoring.

The immediate changes in shrub cover and height that were documented indicate shrubs are more resilient to herbivory than herbaceous species, possibly due in part to the absence of competitive introduced shrub species to displace native shrubs. Thus, structural changes within the shrub layer of plant communities in EINP could be expected relatively soon following the removal of herbivory, allowing for more diverse habitat for some wildlife (e.g., avi-fauna).

3.6.4 Understory Production & Utilization

In 1999, both forb SC and shrub CAG varied among exclosure locations ($p<0.05$; Table 3.7), while grass and forb SC varied with grazing treatment ($p<0.05$). In addition, shrub CAG and grass SC varied between vegetation types ($p<0.10$). In the second year of the study (2000), only forb SC varied among exclosures and grazing treatments ($p<0.05$; Table 3.7), while grass SC differed between vegetation types ($p<0.10$).

The immediate increase in grass and forb SC on protected sites in 1999 (Table 3.7) is indicative of direct herb release from grazing. That is, lower SC values on grazed areas reflect the removal of vegetation during the growing season by herbivores. This contrasts with the response of shrubs, which increased their height and cover rather than CAG. In other words, shrubs seem to have allocated more resources to growing longer twigs, rather than more twigs, after the removal of herbivory..

Comparison of grassland plant community SC and CAG after one and two years of protection from grazing showed a significant exclosure location effect for all growth forms ($p<0.10$; Table 3.8), as well as a grazing effect on grass SC ($p<0.10$). Exclosure location differences have already been discussed (Tables 3.2, 3.3, 3.4, 3.5, and 3.6). These results may also be due to different moisture regimes at the different locations (Table 3.2), as precipitation has been found to greatly influence production on uplands in the Park (Bork et al. 2001).

The response of grass SC to protection from grazing appeared to vary with the duration of protection (Table 3.8). Unsurprisingly, grasslands exposed to herbivory produced the least above-ground SC. However, those protected from grazing for one

growing season produced the most SC (Table 3.8), with two years of protection resulting in intermediate levels of SC.

These results suggest that while heavy grazing in EINP may reduce grass production, some herbivory may be beneficial to maintain growth. This concept is supported by Tracy and McNaughton (1997), Willms et al. (1993), and Towne and Owensby (1984), who all found that litter accumulation and other microsite changes resulting from the removal of ungulate herbivory could reduce grassland production to levels similar to those under heavy grazing. The results found here may also be due to grasslands within the Park being dominated by rhizomatous invaders (e.g., *Poa pratensis*), which become sod-bound relatively quickly after the removal of grazing. Alternatively, rested vegetation may be increasing root growth during the second year of rest, accounting for the decrease in above-ground SC. In addition, grazing may have indirectly increased SC by reducing litter and increasing soil temperature in early spring when plants are initiating growth. In general, light grazing intensities have been recommended for optimal grassland production (Willms et al. 1985). While it is likely that light grazing of grasslands in Elk Island National Park may result in optimal phytomass production, this concept was not addressed by this research and further studies would be required to determine appropriate stocking rates to achieve those utilization levels. In addition, although optimal phytomass production may aid with ungulate management, this is not a primary goal of Park management.

3.6.5 Exotic Species Removal

The response of native plant species to the removal of direct competition from exotic species varied significantly with exclosure location (Table 3.9). After one year of reduced competition, shrub cover varied significantly among locations ($p<0.10$; Table 3.9), but remained similar among species removal treatments. Similarly, native grass and forb cover, as well as native grass density were different among exclosure locations in 2000 ($p<0.10$; Table 3.9), while no species removal effects were observed. However, 1999 forb cover as well as 2000 forb density and shrub cover responded to the exclosure location by species removal interaction ($p<0.05$; Table 3.9). Variation between locations has already been discussed.

The general lack of native plant response to the removal of competition from exotic plants suggests that there is little advantage to using glyphosphate to remove exotic species, as chemical application could not be selective enough to protect native species. The data in Table 3.9 indicate that application of glyphosphate and subsequent weeding slightly reduced native species cover and density in both years of the study. Other factors such as plant community resilience and the duration of the study may also contribute to the lack of response observed. Other data gathered here indicate that grassland plant community resilience in EINP is low. It is also likely that the density of native plant seeds in the seedbank is limited, resulting in sparse recruitment of native plants, even when competition from exotic species is removed. For example, in the fescue grassland, native seedbank levels have been found to be very low following heavy grazing (Willms and Quinton 1995). Alternatively, native plant seeds may be present in the soil seedbank, but require different growing conditions than those present in the exotic species removal

plots, particularly during the two years of the study. For example, exotic species removal led to increased bare soil in some plots, and may have resulted in drier micro-climates and reduced native plant germination and/or establishment.

3.7 Conclusion

The limited response observed within plant communities of Elk Island National Park to the removal of herbivory indicates that the short-term (e.g., 2 year) resilience of these native plant communities is low. While shrub height and cover, as well as native species richness, and grass and forb standing crop showed immediate increases following protection from herbivory, species composition and diversity, particularly of native plants, did not respond, even with the removal of exotic species. Bork et al. (1997a) developed a state-and-transition model of upland plant communities within the Park that suggested invasive dominated grasslands were unlikely to return to native plant communities under natural conditions. The results found here tend to corroborate that model, at least in the short-term. These results are also similar to previous studies that indicate the recovery of native plant communities after prolonged heavy grazing is a long-term endeavour (Trottier 1986; McLean and Tisdale 1972; Pegau 1970), and in some cases, is improbable without a marked reduction in grazing and/or active rehabilitative measures (e.g., seeding of native species) (Trottier 1986).

Removal of herbivory may facilitate the recovery of native plant communities within EINP in the long-term (20 to 40 years). However, complete removal of the Park's ungulate populations is unlikely given the Park's mandate and historical management trends. While a reduction in herbivore populations may benefit plant communities within

the Park, the results of this action were not addressed by this study. Although

rehabilitative measures documented by other studies (Trottier 1986) may prove useful in

EINP, further research is needed before specific recommendations can be made.

Additionally, high variation in ecosite, overstory, and understory characteristics among

exclosures highlights the great level of heterogeneity found throughout the Park, which

needs to be considered in any interpretation of long-term monitoring data.

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Table 3.1: Approximate ungulate populations in the Main Park and Isolation Areas of EINP for the period 1910 to 1999 [values compiled from Blyth (1995) and Parks Canada (1999)].

Ungulate Species	1910	1920	1930	1940	1950	1960	1970	1980	1990	1999
Main Park (13600 ha)										
Moose	19	70	400	113	272	83	280	380	231	250
Elk	30	200	467	473	800	154	350	500	872	1450
Plains Bison	45	200	716	995	1350	750	831	421	444	638
Mule Deer	30	150	200	27	150	0	-	-	-	-
Whitetail Deer	-	-	-	-	1	90	74	120	201	150
Isolation Area (5800 ha)										
Moose	-	-	-	-	-	80	225	100	77	90
Elk	-	-	-	-	-	90	25	75	320	420
Plains Bison	-	-	-	-	75	236	0	-	-	-
Wood Bison	-	-	-	-	-	-	32	110	232	405
Whitetail Deer	-	-	-	-	-	155	265	130	65	60
Total (19400 ha)	124	620	1783	1608	2648	1638	2082	1836	2442	3463*

* Equivalent to a year-long stocking rate of about 2.0 AUM/ha throughout the Park.

Table 3.2: Summary ecosite descriptions for protected and grazed plant communities at each of the six exclosures investigated.

Exclosure Location	Vegetation Type	Grazing Treatment	Slope (%)	Aspect (°)	1999 Rainfall (mm)	2000 Rainfall (mm)	Soil Classification**	Depth of Ah/Ahe/Ae (cm)	Soil Texture*
NORTH LMU:									
Astotin	Grassland	Protected	8	279	330	264	Dark Gray Luvisol	14/13/22	L
		Grazed	8	224					L to SiL
	Forest	Protected	13	222			Dark Gray Luvisol	0/7/20	L
		Browsed	13	274					L
Boreal	Grassland	Protected	15	207	141	178	Dark Gray Luvisol	0/24/8	SL
		Grazed	13	188					SL
	Forest	Protected	16	20			Dark Gray Luvisol	10/0/15	L to SL
		Browsed	19	0					SL
CENTRAL LMU:									
Shirley	Grassland	Protected	10	193	172	175	Gray Luvisol	0/0/8	CL
		Grazed	11	175					CL
	Forest	Protected	16	324			Gray Luvisol	0/0/9	C
		Browsed	20	307					CL
Tawayik	Grassland	Protected	8	183	193	227	Dark Gray Luvisol	8.5/0/5	L
		Grazed	10	174					L
	Forest	Protected	0	n/a			Gray Luvisol	0/0/8	L
		Browsed	0	n/a					L to SL
SOUTH LMU:									
Ranger	Grassland	Protected	18	146	180	208	Dark Brown Chernozem	23/0/0	SL
		Grazed	14	124					L
	Forest	Protected	11	350			Dark Gray Luvisol	0/9/24	SL
		Browsed	15	316					SL
Bailey	Grassland	Protected	5	297	187	198	Gray Luvisol	0/0/10	S
		Grazed	1	n/a					S
	Forest	Protected	7	41			Gray Luvisol	0/0/14	S to LS
		Browsed	3	338					S to LS

* L = loam, C = clay, CL = clay loam, SiL = silty loam, S = sand, SL = sandy loam, LS = loamy sand.
** The Canadian System of Soil Classification (1998)

Table 3.3: Results of split-plot ANOVA analysis (F value & significance) for the effects of exclosure location, grazing, and vegetation type on soil properties [mean ± (SE)] at a depth of 0 – 15 cm in Elk Island National Park (2000).

ANOVA	df	Ammonium (ppm)	Bulk Density (g/cm³)	Calcium (ppm)	Electrical Conductivity (dS/m)	Magnesium (ppm)	Organic Matter (%)	pH	Phosphorous (ppm)	Potassium (ppm)	Sulphate (ppm)
Exclosure Location(E)	5	$F = 1.47$	$F = 4.79*$	$F = 90.91***$	$F = 11.39***$	$F = 75.25***$	$F = 19.83***$	$F = 6.27**$	$F = 11.47*$	$F = 16.69***$	$F = 5.54**$
Astotin		1.7 (0.3)	0.91 (0.05)a	2065 (159)b	0.24 (0.02)ab	167 (16)b	4.3 (0.5)b	6.0 (0.1)a	33.8 (13.7)ab	124 (10)b	4.1 (0.3)b
Boreal		2.5 (0.9)	0.81 (0.09)ab	1885 (117)b	0.28 (0.02)a	234 (30)b	5.1 (0.7)b	6.0 (0.1)a	11.6 (3.7)b	113 (12)b	5.3 (0.5)b
Shirley		1.6 (0.2)	0.61 (0.02)b	3430 (213)a	0.35 (0.03)a	732 (60)a	10.2 (1.5)a	6.0 (0.1)a	16.3 (8.2)ab	379 (58)a	10.3 (1.9)a
Tawayik		1.5 (0.2)	0.80 (0.03)ab	2008 (177)b	0.27 (0.04)a	186 (26)b	5.2 (1.1)b	6.0 (0.1)a	23.4 (10.7)ab	168 (32)b	4.1 (0.6)b
Ranger		4.0 (1.7)	0.85 (0.05)ab	2277 (359)b	0.25 (0.01)a	253 (58)b	4.5 (1.0)b	6.2 (0.1)a	32.0 (16.7)ab	153 (27)b	4.5 (0.3)b
Bailey		1.5 (0.3)	0.74 (0.08)ab	343 (59)c	0.12 (0.02)b	50 (8)b	1.0 (0.3)b	5.4 (0.1)b	55.6 (6.8)a	38 (8)b	2.3 (0.6)b
Grazing (G)	1	$F = 1.94$	$F = 0.002$	$F = 0.52$	$F = 1.93$	$F = 1.68$	$F = 0.14$	$F = 0.21$	$F = 0.05$	$F = 0.03$	$F = 0.99$
Protected		1.7 (0.2)	0.79 (0.05)	2032 (295)	0.24 (0.02)	285 (73)	5.13 (1.02)	5.9 (0.1)	29.2 (7.0)	160 (32)	4.6 (0.6)
Grazed		2.6 (0.7)	0.79 (0.04)	1970 (289)	0.26 (0.03)	256 (63)	4.92 (0.89)	5.9 (0.1)	28.4 (7.3)	164 (38)	5.6 (1.1)
E x G (Error 1)	5	$F = 1.01$	$F = 0.45$	$F = 0.21$	$F = 0.61$	$F = 0.39$	$F = 0.36$	$F = 1.37$	$F = 0.22$	$F = 0.99$	$F = 2.28$
Veg Type (VT)	1	$F = 0.56$	$F = 0.16$	$F = 1.76$	$F = 0.64$	$F = 0.98$	$F = 0.20$	$F = 3.40*$	$F = 10.71***$	$F = 4.95**$	$F = 0.83$
Forest		1.9 (0.3)	0.77 (0.05)	1878 (192)	0.26 (0.02)	252 (75)	5.23 (1.13)	5.8 (0.1)b	41.9 (5.3)a	188 (41)a	5.4 (1.0)
Grassland		2.4 (0.7)	0.79 (0.04)	2124 (287)	0.24 (0.02)	288 (60)	4.82 (0.73)	6.0 (0.1)a	15.6 (6.5)b	136 (26)b	4.8 (0.8)
G x VT	1	$F = 0.01$	$F = 0.08$	$F = 1.50$	$F = 0.34$	$F = 0.12$	$F = 0.72$	$F = 0.58$	$F = 0.13$	$F = 0.25$	$F = 0.32$

*, **, *** Significant at $p<0.10$, $p<0.05$, and $p<0.01$, respectively.

Note: Means with different lower case letters indicate significant differences among means within each soil variable and treatment combination ($p<0.10$).

Table 3.4: Results of split-plot ANOVA analysis (F values & significance) for the effects of exclosure location, grazing, and vegetation type on overstory and shrub parameters [means ± (SE)] in Elk Island National Park. (2000).

ANOVA	df	Tree Canopy Cover (%)	Tree DBH (cm)	Tree Density (stems/400m²)	Tree Regeneration (stems/m²)	Tree Height (m)	Maximum Shrub Height# (cm)	Shrub Cover[a] (%)	Shrub Density (stems/m²)	Shrub Diversity Indices
Exclosure Location (E)	5	$F = 5.97$**	$F = 0.60$	$F = 37.13$***	$F = 6.19$**	$F = 0.51$	$F = 51.46$***	$F = 37.76$***	$F = 2.50$	$F = 1.64$
Astotin		5 (2)b	15.4 (6.2)	6 (2)b	0.8 (0.3)	11.7 (4.0)	135.4 (119.9)a	66.6 (20.4)a	25.3 (9.7)	0.60 (0.13)
Boreal		49 (19)a	14.9 (6.2)	29 (15)ab	0.7 (0.3)	12.5 (4.2)	119.5 (11.3)ab	71.8 (8.2)a	26.0 (4.1)	0.63 (0.07)
Shirley		21 (13)ab	11.8 (7.0)	14 (9)ab	1.7 (0.8)	7.9 (4.6)	94.4 (23.1)ab	58.8 (10.5)a	29.3 (3.7)	0.61 (0.03)
Tawayik		37 (22)ab	6.6 (3.8)	39 (23)a	0.6 (0.2)	10.1 (6.0)	66.6 (25.9)b	20.3 (7.6)b	10.5 (1.5)	0.58 (0.14)
Ranger		25 (15)ab	11.0 (6.4)	10 (6)b	0.9 (0.5)	8.3 (4.8)	76.5 (16.1)b	43.3 (5.0)ab	23.3 (3.2)	0.65 (0.10)
Bailey		19 (11)ab	10.4 (6.0)	10 (4)b	2.2 (0.5)	7.3 (4.3)	71.9 (12.2)b	31.8 (8.7)ab	31.4 (6.7)	0.66 (0.07)
Grazing (G)	1	$F = 0.25$	$F = 3.34$	$F = 0.89$	$F = 0.01$	$F = 0.04$	$F = 73.64$***	$F = 0.25$	$F = 0.31$	$F = 0.91$
Protected		25 (9)	8.5 (2.7)	19 (7)	1.2 (0.3)	9.4 (2.4)	107.7 (12.8)a	51.1 (7.7)	23.2 (3.5)	0.63 (0.05)
Grazed		27 (9)	14.8 (3.5)	17 (7)	1.1 (0.3)	10.0 (2.6)	80.4 (10.7)b	46.4 (8.4)	25.4 (3.5)	0.61 (0.05)
E x G (Error 1)	5	$F = 0.51$	$F = 0.83$	$F = 0.05$	$F = 0.19$	$F = 0.59$	$F = 0.09$	$F = 0.10$	$F = 0.52$	$F = 0.04$
Veg Type (VT)	1	$F = 41.17$***	$F = 12.89$***	$F = 16.09$***	$F = 0.33$	$F = 12.66$***	$F = 19.18$***	$F = 7.43$**	$F = 0.29$	$F = 0.88$
Forest		49 (3)a	18.4 (1.4)a	34 (8)a	1.3 (0.3)	15.3 (1.6)a	117.6 (9.7)a	59.0 (7.0)a	25.7 (3.5)	0.67 (0.05)
Grassland		3 (3)b	4.9 (3.3)b	2 (1)b	1.0 (0.3)	4.0 (2.1)b	70.5 (10.9)b	38.5 (7.9)b	22.9 (3.5)	0.57 (0.05)
G x VT	1	$F = 0.29$	$F = 0.91$	$F = 0.21$	$F = 0.29$	$F = 0.28$	$F = 0.93$	$F = 0.002$	$F = 0.07$	$F = 0.42$

[a] Analysis performed on log transformed data.

*, **, *** Significant at $p < 0.10$, $p < 0.05$, and $p < 0.01$, respectively.

Shrub height was also significant for exclosure, grazing and plant community in 1999, but even more significant in 2000.

Note: Means with different lower case letters indicate means differ significantly within each overstory/shrub variable and treatment combination ($p < 0.10$).

Table 3.5: Results of split-plot ANOVA analysis (F values & significance) for the effects of exclosure location, grazing, and vegetation type on herbaceous species composition and structure [means ± (SE)] in Elk Island National Park during each of 1999 and 2000.

ANOVA	df	Exotic Species Cover (%) 1999	Exotic Species Cover (%) 2000	Native Species Cover (%) 1999	Native Species Cover (%) 2000	Litter Cover (%) 2000	Herb Height (cm) 2000	Native Herb Species Diversity Indices (2000)	Exotic Herb Species Diversity Indices (2000)	Native Herb Species Richness (2000)	Exotic Herb Species Richness (2000)
Exclosure Location (E)	5	$F = 5.54^{**}$	$F = 4.37^{*}$	$F = 1.25$	$F = 0.29$	$F = 4.61^{*}$	$F = 1.47$	$F = 1.18$	$F = 5.45^{**}$	$F = 21.41^{***}$	$F = 11.20^{***}$
Astotin		4.4 (3.2)bc	1.8 (1.1)b	65.2 (13.3)	45.6 (9.2)	79.2 (8.4)ab	101.9 (7.6)	1.08 (0.03)	0.21 (0.11)	27.5 (2.2)	2.5 (0.7)ab
Boreal		1.0 (0.7)c	0.3 (0.2)b	38.3 (10.1)	39.8 (4.9)	91.9 (1.3)a	103.3 (6.5)	1.00 (0.07)	0.07 (0.07)	21.0 (2.4)	1.5 (0.7)b
Shirley		11.6 (5.4)bc	8.2 (6.0)b	53.6 (8.1)	39.7 (5.5)	81.1 (12.3)ab	84.1 (24.7)	0.97 (0.04)	0.21 (0.13)	21.3 (2.3)	3.3 (1.1)ab
Tawayik		36.0 (20.4)a	36.1 (20.0)a	54.6 (5.8)	44.6 (19.0)	64.6 (17.1)b	81.2 (11.4)	0.93 (0.05)	0.44 (0.10)	17.5 (2.8)	5.0 (0.6)a
Ranger		25.2 (13.1)ab	19.4 (10.9)ab	52.6 (8.3)	47.0 (8.7)	59.7 (17.1)b	82.0 (16.8)	1.01 (0.13)	0.41 (0.04)	23.5 (2.1)	3.8 (0.9)ab
Bailey		7.7 (4.5)b	1.9 (0.7)b	46.4 (6.4)	42.6 (6.4)	63.6 (14.8)b	62.5 (8.2)	1.12 (0.05)	0.14 (0.05)	25.5 (1.5)	1.5 (0.5)b
Grazing (G)	1	$F = 1.36$	$F = 0.79$	$F = 0.05$	$F = 0.02$	$F = 0.89$	$F = 1.52$	$F = 0.97$	$F = 0.60$	$F = 12.80^{**}$	$F = 0.25$
Protected		11.6 (4.7)	8.9 (4.7)	52.5 (5.1)	42.9 (4.5)	75.6 (7.8)	92.1 (8.2)	1.05 (0.04)	0.27 (0.06)	23.8 (1.4)	2.8 (0.5)
Grazed		17.1 (8.0)	13.7 (7.6)	51.1 (5.6)	43.5 (6.1)	71.1 (7.5)	79.5 (8.2)	0.99 (0.04)	0.23 (0.06)	21.6 (1.6)	3.0 (0.6)
E x G (Error 1)	5	$F = 0.39$	$F = 0.53$	$F = 0.73$	$F = 0.25$	$F = 0.38$	$F = 1.16$	$F = 1.38$	$F = 0.51$	$F = 0.08$	$F = 0.34$
Veg Type (VT)	1	$F = 10.07^{***}$	$F = 6.28^{**}$	$F = 2.76$	$F = 3.24^{*}$	$F = 21.48^{***}$	$F = 9.00^{**}$	$F = 8.82^{**}$	$F = 3.90^{*}$	$F = 0.41$	$F = 6.98^{**}$
Forest		2.4 (0.8)b	1.9 (0.8)b	45.4 (4.7)	51.5 (4.3)a	91.4 (1.2)a	100.0 (6.8)a	1.09 (0.03)a	0.18 (0.05)b	23.4 (0.5)	2.2 (0.3)b
Grassland		26.2 (7.8)a	20.7 (8.0)a	58.2 (5.2)	34.9 (5.1)b	55.3 (7.6)b	71.6 (7.7)b	0.95 (0.04)b	0.32 (0.06)a	22.0 (2.1)	3.7 (0.6)a
G x VT	1	$F = 0.41$	$F = 0.38$	$F = 0.002$	$F = 0.41$	$F = 0.25$	$F = 0.02$	$F = 0.75$	$F = 0.80$	$F = 0.41$	$F = 2.16$

*, **, *** Significant at $p<0.10$, $p<0.05$, and $p<0.01$, respectively.

Note: Growth forms and functional groups did not yield any significant results beyond the results shown here. Exclosure and vegetation type were significant in some cases, but not in others. Grazing was never significant. Means with different lower case letters indicate means significantly differ within each understory variable and treatment combination ($p<0.10$).

Table 3.6: Mean percent cover of major plant species (e.g., minimum 1% cover) found in each vegetation type investigated in 2000.

Plant Species	Ranger Grassland Protected	Ranger Grassland Grazed	Ranger Forest Protected	Ranger Forest Grazed	Boreal Grassland Protected	Boreal Grassland Grazed	Boreal Forest Protected	Boreal Forest Grazed	Astotin Grassland Protected	Astotin Grassland Grazed	Astotin Forest Protected	Astotin Forest Grazed
Grasses:												
Agropyron spp.	0.9	0.9	-	-	-	-	-	-	-	-	-	-
Calamagrostis canadensis	-	-	3.6	2.8	16.9	7.0	0.7	2.4	13.7	3.7	0.4	2.1
Carex spp.	0.2	-	-	-	-	-	-	-	-	0.3	0.1	-
Festuca halii (Vasey) Piper	-	-	-	-	-	-	-	-	-	-	-	-
Poa pratensis L. *	21.9	14.9	0.6	0.1	-	0.2	-	-	0.1	2.6	-	-
Phleum pratense L. *	0.8	0.8	-	-	-	-	-	-	-	-	-	-
Schizachne purpurascens (Torr.) Swallen	1.9	0.4	0.9	1.3	0.5	0.4	0.3	-	-	3.6	1.4	2.7
Total Grasses	25.7	17.0	5.1	4.2	17.4	7.6	1.0	2.4	13.8	10.2	1.9	4.8
Forbs:												
Achillea millefolium L.	1.5	0.5	-	-	-	-	-	-	-	0.1	-	-
Agrimonia striata Michx.	4.9	7.7	0.1	0.2	-	-	0.3	-	-	2.0	-	-
Aralia nudicaulis L.	-	-	5.9	4.6	3.0	1.3	7.4	5.3	9.1	28.6	9.8	4.9
Aster spp.	0.9	0.6	4.6	3.0	4.8	1.9	3.0	7.0	7.4	2.1	0.7	0.6
Cornus canadensis L.	-	-	8.3	-	0.1	2.2	3.3	7.7	1.3	0.4	0.6	-
Fragaria virginiana Duchesne	2.8	3.9	3.9	4.3	1.1	2.6	2.0	1.1	0.9	1.1	0.1	0.1
Galium boreale L.	2.6	1.3	3.2	5.8	2.0	2.0	1.0	2.4	2.1	3.3	0.9	1.2
Lathyrus spp.	-	0.2	4.4	4.0	1.1	1.7	9.5	4.4	-	1.0	0.2	-
Plantago major L. *	0.2	0.3	0.7	-	-	-	-	0.5	1.9	0.9	0.1	-
Pyrola asarifolia Michx.	-	-	6.2	1.8	-	0.1	2.1	1.4	0.3	1.3	2.1	0.4
Rubus pubescens Raf.	-	-	4.3	6.4	0.3	5.0	8.4	2.8	2.1	3.3	0.6	3.4
Solidago canadensis L.	1.8	1.1	0.3	6.1	4.0	-	-	-	-	-	-	-
Taraxacum officinale Weber*	11.2	4.0	-	-	-	-	0.2	0.3	-	1.2	0.1	0.1
Trifolium spp. *	1.9	8.3	1.6	-	-	-	0.1	-	-	0.1	-	-
Vicia americana Muhl.	0.9	-	2.0	1.2	0.3	0.6	-	0.5	2.3	0.7	1.3	0.1
Total Forbs	28.7	27.9	45.5	37.4	16.7	17.4	37.3	33.7	29.5	45.9	16.5	10.8
Shrubs & Tree Saplings												
Amelanchier alnifolia Nutt.	1.1	0.4	0.7	0.5	3.5	3.2	2.8	4.4	1.9	0.6	0.9	1.9
Corylus cornuta Marsh.	-	-	5.3	-	54.9	59.1	34.8	28.6	8.3	4.2	80.8	80.0
Populus balsamifera L.	-	-	-	0.6	0.6	-	0.1	0.1	3.6	3.4	3.6	-
Populus tremuloides Michx.	1.1	0.1	10.4	4.1	4.4	1.6	1.4	0.8	0.9	2.3	-	0.3
Prunus virginiana L.	5.3	0.9	1.2	0.1	3.3	2.6	2.4	0.9	2.9	6.3	1.6	3.4
Rosa woodsii Lindl.	4.8	1.9	8.2	7.1	1.2	1.2	2.5	1.9	6.5	1.4	0.9	0.1
Rubus idaeus L.	-	15.7	11.9	10.2	-	6.2	1.1	3.6	1.4	-	2.1	1.7
Shepherdia canadensis (L.) Nutt.	-	-	4.7	-	-	-	6.3	-	-	-	-	-
Symphoricarpos occidentalis Hook.	25.8	16.3	5.2	5.7	6.7	12.6	7.4	1.5	0.8	8.1	9.0	7.6
Vaccinium myrtelloides Michx.	-	-	-	-	-	-	-	-	-	-	-	-
Viburnum edule (Michx.) Raf.	-	-	3.1	0.2	-	-	0.9	3.9	0.3	-	-	-
Total Shrubs & Saplings	38.1	35.3	50.7	28.5	74.6	86.5	59.7	45.7	26.6	26.3	97.3	95.0
Litter Cover	25.3	35.3	90.5	87.8	95.5	90.6	89.4	92.2	78.4	56.3	95.3	86.8

* Indicates exotic species

Table 3.6 (continued): Mean percent cover of major plant species (e.g., minimum 1% cover) found in each vegetation type investigated in 2000.

Plant Species	Shirley Grassland Protected	Shirley Grassland Grazed	Shirley Forest Protected	Shirley Forest Grazed	Tawayik Grassland Protected	Tawayik Grassland Grazed	Tawayik Forest Protected	Tawayik Forest Grazed	Bailey Grassland Protected	Bailey Grassland Grazed	Bailey Forest Protected	Bailey Forest Grazed
Grasses:												
Agropyron spp.	0.3	1.5	-	0.1	-	0.2	0.4	-	0.3	0.1	-	-
Calamagrostis canadensis	-	-	1.3	3.1	-	-	3.3	0.4	-	-	6.0	9.1
Carex spp.	1.1	0.6	-	-	0.1	0.2	-	-	6.5	3.5	1.8	1.3
Festuca hallii (Vasey) Piper	-	-	-	-	-	-	-	-	0.2	-	-	0.3
Poa pratensis L.*	2.9	19.1	-	-	4.2	21.6	-	0.1	0.3	1.9	0.3	-
Phleum pratense L.*	1.1	0.1	-	-	1.9	2.6	0.2	-	-	-	-	-
Schizachne purpurascens (Torr.) Swallen	1.1	-	0.8	0.4	-	-	-	1.5	0.9	1.1	4.1	5.6
Total Grasses	6.5	21.3	2.1	3.6	6.2	24.6	3.9	2.0	8.2	6.6	12.2	16.3
Forbs:												
Achillea millefolium L.	2.9	4.9	-	-	6.4	2.8	-	-	2.6	5.3	1.2	0.6
Agrimonia striata Michx.	0.9	1.6	-	-	-	0.7	1.3	-	0.3	-	-	-
Aralia nudicaulis L.	-	-	19.9	14.7	0.5	-	14.3	32.4	0.1	-	4.3	9.1
Aster spp.	5.4	3.0	2.8	2.8	0.9	0.8	1.4	2.5	2.6	0.5	0.9	0.9
Cornus canadensis L.	-	-	2.7	1.8	-	-	15.9	6.9	4.4	0.1	3.9	9.9
Fragaria virginiana Duchesne	19.6	8.8	0.6	2.3	0.8	0.8	4.2	3.5	1.4	1.4	5.1	4.2
Galium boreale L.	8.2	0.8	2.4	1.9	0.5	1.3	2.7	1.9	1.8	0.1	1.7	0.8
Lathyrus spp.	2.0	0.9	5.0	1.0	-	-	3.4	1.9	0.6	1.2	3.5	3.8
Plantago major L.*	-	-	0.2	0.6	3.3	3.0	0.8	0.3	-	-	-	-
Pyrola asarifolia Michx.	-	-	-	-	-	-	0.2	1.5	0.3	-	2.5	0.5
Rubus pubescens Raf.	-	-	6.4	1.8	-	-	2.1	3.6	-	-	0.5	1.0
Solidago canadensis L.	0.3	-	-	-	-	-	-	-	-	-	-	-
Taraxacum officinale Weber*	0.3	0.6	-	-	18.9	11.6	0.7	0.4	-	-	-	-
Trifolium spp.*	1.5	6.3	-	-	20.4	52.4	1.7	9.0	1.6	0.4	3.2	-
Vicia americana Muhl.	1.3	1.6	0.3	0.8	1.2	1.0	5.9	1.2	1.5	1.1	1.6	1.5
Total Forbs	42.4	28.5	40.3	27.7	52.9	74.4	54.6	65.1	17.2	10.1	28.4	32.3
Shrubs & Tree Saplings												
Amelanchier alnifolia Nutt.	1.9	2.3	2.6	4.9	-	-	-	0.6	0.6	4.3	4.1	2.9
Corylus cornuta Marsh.	-	-	28.5	49.1	-	0.6	0.6	7.0	-	-	5.0	1.7
Populus balsamifera L.	-	0.1	0.2	-	5.3	0.4	0.8	-	-	0.2	-	-
Populus tremuloides Michx.	-	-	22.0	8.3	3.1	-	4.5	1.7	6.9	3.6	7.3	3.4
Prunus virginiana L.	24.8	8.5	0.8	1.1	-	-	-	0.3	-	-	1.1	-
Rosa woodsii Lindl.	11.0	7.4	4.7	4.1	-	-	7.4	8.1	-	0.7	0.7	0.8
Rubus idaeus L.	4.7	0.7	7.1	3.0	-	-	7.3	2.6	-	-	0.5	-
Shepherdia canadensis (L.) Nutt.	-	-	-	-	-	-	10.0	4.3	-	-	5.3	-
Symphoricarpos occidentalis Hook.	22.7	8.2	0.5	0.4	5.3	4.2	1.8	5.3	2.7	0.9	0.6	-
Vaccinium myrtilloides Michx.	-	-	-	-	-	-	-	-	4.3	4.0	20.2	30.9
Viburnum edule (Michx.) Raf.	-	-	0.1	0.4	-	-	-	-	0.1	-	3.9	0.7
Total Shrubs & Saplings	65.1	27.2	66.5	71.3	13.7	5.2	32.4	29.9	14.6	13.7	48.7	40.4
Litter Cover	85.6	45.0	96.0	97.7	46.3	25.6	89.7	96.6	26.1	53.8	89.3	85.3

* Indicates exotic species

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Table 3.7: Results of split-plot ANOVA analysis (F values & significance) for the effects of exclosure, grazing and vegetation type on standing crop (SC) of grasses and forbs, and shrub current annual growth (CAG) [mean ± (SE)] in EINP during 1999 and 2000.

ANOVA	df	Grass SC (kg/ha) 1999	Grass SC (kg/ha) 2000	Forb SC (kg/ha) 1999	Forb SC (kg/ha) 2000	Shrub CAG[a] (kg/ha) 1999	Shrub CAG[a] (kg/ha) 2000
Exclosure Location (E)	5	$F=3.18$	$F=2.15$	$F=5.65^{**}$	$F=9.26^{**}$	$F=7.91^{**}$	$F=2.79$
Astotin		812.4 (381.7)	1172.0 (553.2)	607.1 (204.6)ab	529.2 (146.8)b	1687.2 (808.8)a	1189.2 (486.8)
Boreal		786.3 (381.3)	681.2 (300.8)	455.5 (74.9)b	342.0 (95.2)b	1507.7 (478.2)a	1061.2 (353.6)
Shirley		699.6 (221.0)	783.2 (181.6)	529.4 (110.9)ab	575.2 (82.0)b	907.6 (266.8)ab	1345.2 (526.0)
Tawayik		365.6 (113.7)	496.0 (118.0)	533.4 (132.3)ab	992.0 (178.0)a	410.3 (178.6)b	252.4 (137.2)
Ranger		679.4 (123.1)	745.2 (96.0)	864.4 (219.8)a	867.2 (96.4)a	569.3 (120.2)ab	735.2 (104.0)
Bailey		900.9 (105.0)	780.0 (169.2)	371.9 (69.9)b	403.2 (36.8)b	273.9 (105.0)b	424.0 (116.8)
Grazing (G)	1	$F=7.04^{**}$	$F=2.91$	$F=20.61^{***}$	$F=12.86^{**}$	$F=0.19$	$F=2.93$
Protected		819.7 (165.5)a	881.2 (192.8)	692.0 (82.3)a	742.4 (95.2)a	927.4 (260.4)	1019.2 (254.4)
Grazed		594.0 (99.9)b	671.2 (109.6)	428.5 (79.1)b	493.6 (74.0)b	857.9 (283.7)	650.0 (141.6)
E x G	5	$F=0.15$	$F=0.25$	$F=0.20$	$F=0.69$	$F=0.26$	$F=1.19$
Vegetation Type (VT)	1	$F=3.51^{*}$	$F=3.55^{*}$	$F=0.03$	$F=0.42$	$F=3.52^{*}$	$F=6.62^{**}$
Forest		502.8 (112.1)b	545.2 (100.8)b	571.9 (85.6)	591.2 (92.8)	1155.6 (287.9)a	1098.0 (226.4)a
Grassland		911.0 (139.8)a	1007.2 (176.8)a	548.6 (94.0)	645.2 (92.8)	629.7 (230.4)b	570.8 (164.4)b
G x VT	1	$F=0.61$	$F=0.45$	$F=0.51$	$F=0.04$	$F=0.81$	$F=0.14$

[a] Analysis performed on square-root transformed data.
*, **, *** Significant at $p<0.10$, $p<0.05$, and $p<0.01$, respectively.
Note: Means with different lower case letters indicate means significantly differ within each production variable and treatment combination ($p<0.10$).

Table 3.8: Phytomass production [mean ± (SE)] of grassland plant communities in Elk Island National Park in 2000, after one and two years of protection from herbivory.

Main Effects	df	Grass Standing Crop[a] (kg/ha)	Forb Standing Crop[a] (kg/ha)	Shrub CAG (kg/ha)
Exclosure Location (E)	5	$F = 5.00**$	$F = 5.38***$	$F = 3.25*$
Astotin		1856 (388)a	716 (92)ab	436 (108)ab
Boreal		1852 (684)a	172 (56)b	1128 (500)a
Shirley		1180 (156)ab	636 (92)ab	868 (204)ab
Tawayik		692 (136)b	1052 (104)a	36 (20)b
Ranger		644 (60)b	1420 (608)a	624 (16)ab
Bailey		696 (192)b	512 (104)ab	260 (16)ab
Grazing (G)	2	$F = 3.10*$	$F = 2.07$	$F = 1.18$
Protected (2 years)		1196 (88)ab	780 (72)	740 (72)
Protected (1 year)		1448 (100)a	964 (80)	536 (60)
Grazed		820 (72)b	512 (60)	400 (52)
Error (E x G)	10			

[a] Analysis performed on square-root transformed data

*, **, *** Significant at $p<0.10$, $p<0.05$, and $p<0.01$, respectively.

Note: Means with different lower case letters indicate means significantly differ within each production variable and treatment combination ($p<0.10$).

Table 3.9: Results of ANOVA analysis (F values & significance) for the effects of exclosure location and exotic species removal on native plant abundance in grassland plant communities protected from grazing [mean ± (SE)] in EINP.

ANOVA	df	Native Species Cover 1999 (%)			Native Species Cover 2000 (%)			Native Species Density 2000 (#/700 cm²)		
		Grass	Forb[a]	Shrub	Grass	Forb[a]	Shrub	Grass	Forb[a]	Shrub
Exclosure Location (E)	3	F = 4.07	F = 3.42	F = 8.29 *	F = 7.35*	F = 6.51*	F = 0.41	F = 8.93*	F = 4.24	F = 1.21
Shirley		2 (1)	22 (6)	9 (2)ab	2 (1)b	35 (6)a	14 (4)	2 (1)b	8 (1)	2 (0)
Tawayik		0 (0)	3 (1)	1 (0)b	1 (0)b	9 (3)b	13 (7)	1 (1)b	3 (1)	1 (0)
Ranger		2 (1)	8 (3)	21 (7)a	7 (4)b	13 (4)b	27 (8)	7 (4)b	3 (1)	3 (1)
Bailey		12 (4)	18 (3)	3 (2)b	25 (6)a	36 (7)a	13 (5)	40 (10)a	12 (2)	1 (0)
Species Removal (SR)	1	F = 2.01	F = 0.72	F = 0.36	F = 4.33	F = 1.12	F = 0.46	F = 3.02	F = 0.63	F = 0.37
ESR Plot		2 (1)	13 (3)	9 (3)	5 (2)	25 (4)	13 (4)	7 (3)	7 (1)	1 (0)
Untreated Plot		6 (2)	14 (3)	9 (3)	13 (4)	21 (4)	21 (5)	18 (6)	6 (1)	1 (0)
E x SR (Error 1)	3	F = 1.72	F = 3.94***	F = 0.81	F = 1.30	F = 1.28	F = 3.44**	F = 1.47	F = 3.40**	F = 1.76
Shirley ESR		1 (1)	17 (7)ab	13 (3)	1 (1)	33 (9)	19 (6)ab	1 (1)	7 (2)abc	2 (1)
Shirley Untreated		3 (1)	27 (10)a	6 (2)	3 (1)	36 (9)	10 (4)ab	3 (1)	10 (2)ab	1 (0)
Tawayik ESR		0 (0)	1 (1)c	0 (0)	0 (0)	7 (2)	0 (0)b	0 (0)	2 (1)cd	0 (0)
Tawayik Untreated		0 (0)	6 (2)bc	1 (1)	1 (1)	12 (5)	27 (13)ab	2 (2)	3 (1)bd	2 (1)
Ranger ESR		1 (1)	8 (3)bc	16 (7)	0 (0)	13 (4)	34 (11)a	1 (1)	3 (1)bd	3 (1)
Ranger Untreated		3 (2)	9 (5)bc	26 (11)	15 (8)	13 (7)	20 (10)ab	13 (8)	4 (1)bd	3 (1)
Bailey ESR		6 (2)	26 (4)a	1 (1)	17 (5)	48 (11)	1 (1)b	26 (8)	15 (2)a	3 (1)
Bailey Untreated		18 (8)	16 (5)ab	10 (6)	34 (11)	24 (9)	25 (9)ab	54 (17)	9 (3)ab	2 (1)
Error 2	72									

[a] Analysis performed on square-root transformed data

*, **, *** Significant at p<0.10, p<0.05, and p<0.01, respectively.

Note: Means with different lower case letters indicate means differ significantly within each variable and treatment combination (p<0.10).
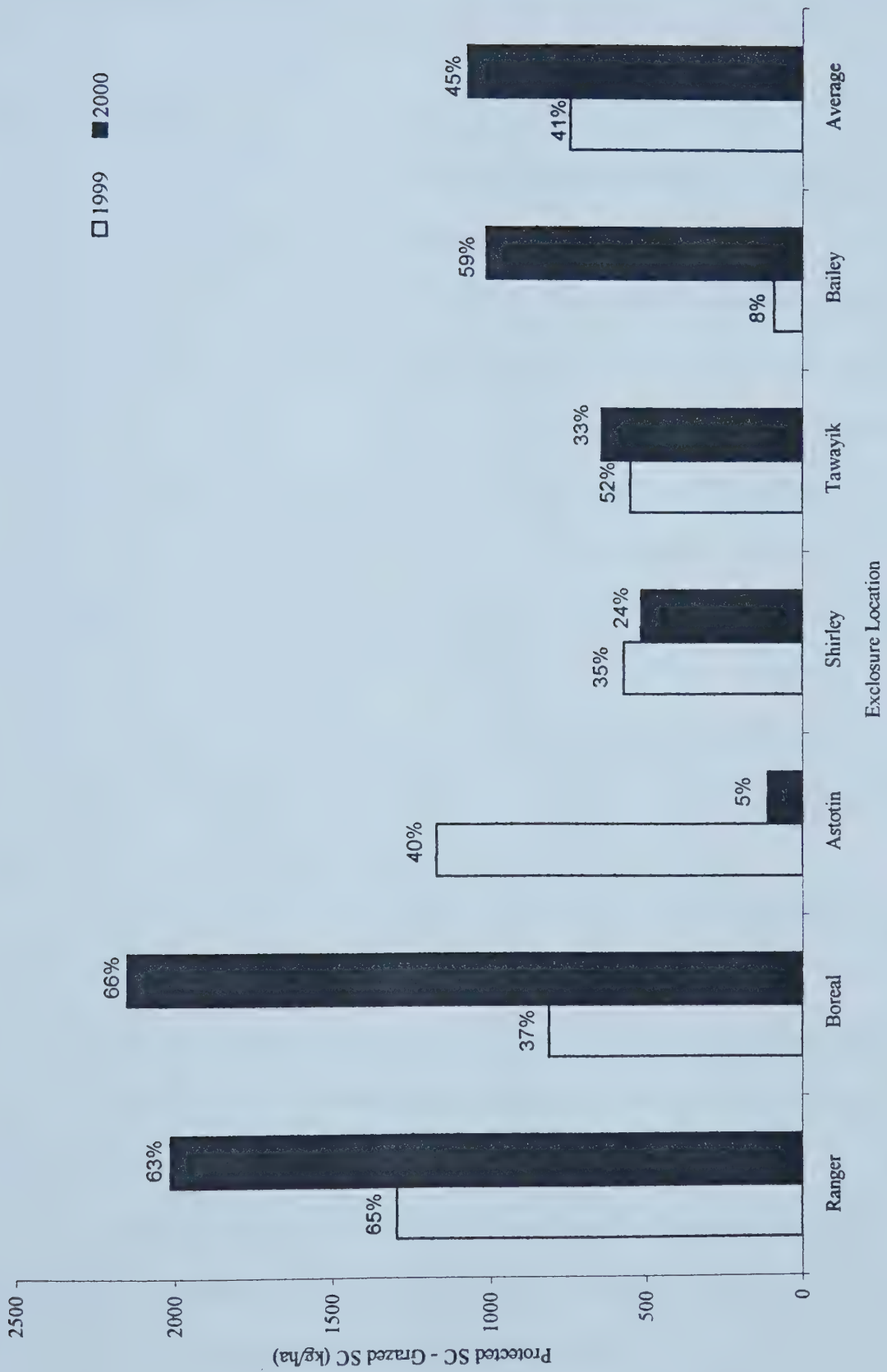
Figure 3.1: Utilization of herbaceous SC in Elk Island National Park, where 1999 utilization is a comparision of SC within exclosures to SC exposed to herbivory, and 2000 utilization is a comparison of SC within range cages to SC exposed to herbivory.

CHAPTER 4: Effects of Grazing on Transplanted *Festuca hallii* (Vasey) Piper in Elk Island National Park

4.1 Introduction

Plains rough fescue is a cool season bunchgrass indigenous to black soils of the northern Mixed Grass and Aspen Parkland ecoregions (Harms 1985; Bailey and Anderson 1978; Coupland and Brayshaw 1953). This is arguably the most productive area of vegetation within the Northern Great Plains, and much of the native vegetation has been lost to cultivation or altered by livestock grazing (Trottier 1986). Historically, these areas provided forage and habitat for bison and other ungulates. Bison, for example, utilized fescue grasslands extensively during the fall and winter following immigration from the southern prairies (Baumeister et al. 1996; Morgan 1980). Rough fescue is a productive, high quality forage that retains up to 76% of its standing crop throughout the winter, making it an excellent dormant season forage (Willms et al. 1985). Horton (1991) found that plains rough fescue maintained crude protein levels greater than 8% throughout the growing season, and 6.5% in the dormant season.

Plains rough fescue is characterized morphologically by clumps that range from 7 to 10 cm in diameter. It may be differentiated from *Festuca campestris* (foothills rough fescue) and *Festuca altaica* (arctic rough fescue) by its deciduous outer leaf blades, densely scabrous leaves, as well as its more frequent occurrence of short, creeping rhizomes (Pavlick and Looman 1984).

A rapidly growing grass that initiates growth early in the spring just after snowmelt, seed production of plains rough fescue occurs at the end of June (Romo et al. 1991; Bailey and Anderson 1978). Because considerable energy is devoted to growth

and reproduction early in the growing season, rough fescue is generally considered very susceptible to defoliation at this time (Horton 1991; Willms et al. 1985). While light to moderate stocking rates may have little effect on range condition (Willms et al. 1985), heavy stocking rates reduce the basal area and seedbank of rough fescue (Willms and Quinton 1995), and may extirpate it from the site completely (Trottier 1986). Protection from herbivory may increase rough fescue if it has not been eliminated. However, recovery of fescue grassland is slow and may take between 20 and 40 years, if the fescue recovers at all (Trottier 1986; Willms et al. 1985; McLean and Tisdale 1972). On sites where plains rough fescue has been extirpated, intensive rehabilitative measures such as seeding, coupled with reductions in grazing pressure, may be required (Trottier 1986). This need appears to be particularly important where invasive exotic plant species have replaced rough fescue, creating an environment unfavourable for natural fescue re-establishment (Willoughby 1997).

While much research has been conducted on the response and recovery of rough fescue to various disturbances including livestock grazing, limited information exists on the ability of fescue to survive under intensive wildlife use. Elk Island National Park (EINP) is located in east-central Alberta within the Aspen Parkland transition zone between Mixed Prairie to the south and Boreal Forest to the north. Due to its small size, fenced perimeter, and lack of major predators, high native ungulate populations have persisted within the Park for many decades (Table 4.1). Intense herbivory has changed plant community composition and structure (Bork et al. 1997b), to include fewer native grass species and greater introduced species such as Kentucky bluegrass (*Poa pratensis* L.) and dandelion (*Taraxacum officinale* Weber) (Bork et al. 1997a). Plains rough fescue

is now known to exist at only one location within the Park, which wasn't discovered until 1993 (Blyth et al. 1993). Given that the Park is mandated to manage for native species, as well as biodiversity (Parks Canada 1988) and plains rough fescue is assumed to have been an important species in the region, there is a need to develop a greater understanding of fescue within the Park, including its response to intensive herbivory.

To assess the potential recovery of this important bunchgrass within EINP under current herbivory levels, a study was designed to quantify and compare the morphological and production responses of fescue plants transplanted into grasslands exposed to ungulate grazing, with those planted in adjacent protective ungulate-proof exclosures. Our hypothesis was that plains rough fescue plants within protected areas would have greater rates of survival and growth, in addition to being more productive than their counterparts outside the exclosures.

4.2 Study Area

Elk Island National Park is a 194 km^2 area situated 37 km east of Edmonton, Alberta (53°37'N, 112°58'W) within the Beaver Hills-Cooking Lake Moraine. The Park is elevated between 30 and 60 m above the surrounding plains (710 to 760 m ASL), and is composed of knob and kettle topography with slopes varying between approximately 0 and 20%. Upland soils are mostly well-drained Orthic Gray Luvisols (Crown 1977), while Dark Gray Luvisols occupy more open areas. Soil textures vary from loam to silty loam or loamy sand.

Located in the cool continental, sub-humid climatic region, EINP receives about 450 mm of precipitation annually, with 75% falling as summer rain (Environment Canada 1993). Temperatures vary from -40°C in winter to 32°C in summer.

Uplands are mostly dominated by aspen (*Populus tremuloides* Michx.) forest, which covers roughly 80% of the Park. The understory consists of a variety of herbs and shrubs, of which marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.) and beaked hazel are the most abundant (Bork et al. 1997a). South-facing slopes and drier sites are dominated by grasslands of primarily introduced plant species including Kentucky bluegrass and dandelion. Elk Island is the only fenced national park in Canada. Substantial ungulate populations are found in the Park, and place great demand on the vegetation all year, as animal migration is restricted by the 2.2 m perimeter fence. In 1999, roughly 640 plains bison (*Bison bison*), 400 wood bison (*Bison athabascae*), 340 moose (*Alces alces*), 1850 elk (*Cervus elaphus*), and fluctuating white-tail and mule deer populations (*Odocoilius virginianus* and *O. hemionus*) were supported by the habitat in EINP (Parks Canada 1999) (Table 4.1). Given that this study is concerned with the effect of grazing on plains rough fescue, a potential source of forage in the Park, it is important to note that these year-long stocking densities are among the highest in North America.

As a result of a Park management workshop held in 1997, the Park has been conceptually divided into three land management units (LMU) to facilitate biological monitoring and management (Equus Consulting Inc. 1997). The south LMU, or Isolation Area, is located south of Highway16, and is physically separate from the Main Park. The central and north LMUs are north of Highway 16. Within each LMU, four long-term bio-

monitoring plots (LTBP) (0.5 by 2 km) have been established for monitoring Elk Island's natural resources (Cool 1999).

4.3 Experimental Design

In the winter of 1998-99 four ungulate proof exclosures, each 20 by 50 m in size, were constructed in EINP. These exclosures were located within the south and central LMUs with two in each area. In addition, each exclosure was situated within a LTBP to complement current bio-monitoring programs. Exclosure fences were 2.2 m tall to exclude all large ungulates.

Exclosure locations were randomly selected within each LTBP, although each exclosure was positioned locally to include a grassland community type. For this study, plot pairs consisted of a grassland plant community divided by the exclosure fence, initially resulting in two areas of similar plant species composition, structure and ecosite characteristics at each exclosure (Table 4.2). Grassland communities outside the exclosures were exposed to continuous year-long grazing while protected grasslands were allowed to recover following the cessation of native ungulate herbivory.

Eighty plains rough fescue plant cores were removed from a native rangeland at the University of Alberta ranch at Kinsella, 100 km southeast of the Park, and transplanted in and adjacent to the four exclosures in early May 1999, before the plants initiated summer growth. Plants were excavated using a soil corer 6.3 cm in diameter and 15 cm long. The soil portion of each core was wrapped in plastic to reduce moisture and soil loss during transport. Cores were subsequently transplanted within 4 days into holes made by the same corer in order to minimize air spaces and ensure a uniform planting

process. Ten fescue cores were systematically transplanted (to facilitate relocation) along a permanently marked 15 m transect established in each exclosure. Specific locations along each transect are given in Appendix 2. Another 10 were planted outside each exclosure using the same technique.

4.4 Vegetation Sampling

Initial tiller counts were taken at the time of transplantation. Fescue tillers per core were then re-counted monthly during the growing seasons of 1999 and 2000 (May through September, inclusive). In addition, utilization estimates based on the number of tillers grazed (0, 50 and 100% use) were made for each plant at the time of each tiller count in 2000. Seedheads produced by each core were counted in July 2000, while maximum fescue height and basal diameter were measured in August 2000. Fescue survival was also documented. A dead fescue plant was defined as one with a zero tiller count for two consecutive months.

Two, separate 15 m transects were located in each plant community to measure species composition and structure. Herbaceous species cover was sampled in eight 0.4 by 0.5 m quadrats at 2 m intervals along each transect (N=16) using the ocular estimation method (Daubenmire 1959). Shrub species cover was similarly estimated within 1 m^2 nested quadrats at the same intervals.

Ecosite data collected within each plant community included slope gradient, aspect, and soils, along with precipitation in each year (Table 4.2). Slope was measured using a clinometre. Soil cores were randomly collected from each grassland community and texture analysis performed using the hydrometer method (McKeague 1978).

4.5 Data Analysis

In this investigation, grazed and ungrazed grassland communities were considered the experimental units at each exclosure, with the latter treated as blocks. Fescue cores represented sub-samples within each community and provided a representative sample of plant responses across the site. Sub-samples were also needed to assess rates of fescue survival per community.

All data were checked for normality and homogeneity using the Shapiro-Wilkes statistic prior to analysis. Fescue tiller counts and maximum fescue height were square-root transformed. Final fescue tiller counts in each year, as well as basal diameter and height data of live plants were then analyzed using a randomized complete block design (Steel et al. 1997). May 1999 and 2000 tiller counts were used as covariates for year-end tiller count analysis in each of their respective years. Exclosure and grazing treatment effects were tested against their interaction, while the variation among individual fescue cores was used to test for the interaction effect. An alpha level of $p<0.10$ was used to determine significant effects. Post-hoc mean comparisons were conducted on all significant variables ($p<0.10$) using Tukey's test.

Analysis was also done to examine fescue tiller demographics throughout the study. Monthly fescue live tiller counts from 1999 and 2000 were analyzed for year, month, covariate, exclosure, and grazing effects, as well as their interactions, using repeated measures multiple ANOVA (SAS 1991). Initial tiller counts (May 1999) were used as covariates.

4.6 Results & Discussion

4.6.1 Fescue Survival & Morphology

Relatively low overall mortality was found for the transplanted fescue plants (Table 4.3). However, the mortalities that did occur were from fescue cores planted within grazed areas where survival was 85% by September 2000, significantly below that of ungrazed cores (p<0.05; Table 4.3). The 15% mortality (6 plants of 80) included 3 deaths before July 1999, with the remaining in August 1999, September 1999, and September 2000. In addition to mortality differences, grazed plants were typically smaller in basal diameter and maximum height by the end of the study in September 2000 (p<0.05; Table 4.3). No exclosure/location-based differences were found for survival, basal diameter, or height measurements (Table 4.3).

The differences in survival and morphology between fescue plants exposed to grazing and those protected from grazing illustrate the negative impact of intensive native ungulate grazing on plains rough fescue growth and development. Although grazing did not eliminate fescue during the 2 years of the study, it clearly reduced the establishment success of transplants, as well as the vigour of remaining live plants. These results support previous research on rough fescue that has found it to be highly sensitive to defoliation during the spring growing season (Horton 1991; Willms et al. 1985), and more greatly affected by intensive grazing (Willms and Quinton 1995; Trottier 1986; Willms et al. 1985).

The number of seedheads produced by plains rough fescue plants was visibly reduced by grazing (Figure 4.1): only one of 34 live fescue plants in grazed areas

produced seedheads in 2000. In contrast, 10 of 40 live fescue plants protected from ungulate grazing produced seed in 2000. Seedhead production is an important recovery mechanism for rough fescue, particularly where plant numbers are low, as it facilitates restoration of the depleted soil seed bank (Willms and Qinton 1995), and the long-term spread of this key bunchgrass.

Seedhead density per plant was particularly high within the Bailey exclosure (Figure 4.1), which may indicate that this site provides better habitat for plains rough fescue growth and survival than other exclosure locations, likely due to differences in soil texture. Soil at the Bailey location is much sandier than other locations (Table 4.2) and may favour rough fescue growth. This conclusion is further supported by plant community composition data (Table 4.4), which shows the Bailey exclosure as the only location where plains rough fescue was present (though sparsely) in the pre-existing plant community. The sandier soil conditions at the Bailey site also appear to limit the abundance of invasive exotic species such as Kentucky bluegrass and clover (*Trifolium* spp.) relative to other locations (Table 4.4). This may allow the fescue plants, both native and transplanted, to be more successful at surviving. These results tend to support the notion that competition from other vegetation may be equally important as site characteristics in limiting fescue growth and spread in grasslands throughout the rest of the Park, although further research is needed to test this.

4.6.2 Tiller Numbers & Dynamics

Initial (May 1999) tiller numbers per plant among the four exclosure locations were relatively similar, ranging from 29 to 37. Despite this, year-end tiller numbers

analyzed in 1999 indicate significant exclosure location effects (Table 4.5). Among the various locations, the Ranger and Shirley exclosures had lower fescue tiller numbers relative to the Tawayik and Bailey exclosures. Although live fescue plants on grazed areas had slightly fewer tillers relative to ungrazed areas, this difference was considered non-significant (Table 4.5). Despite this, a significant covariate effect was found in both years ($p < 0.01$; Table 4.5), indicating plants with more tillers early on were more likely to grow and lead to a greater number of tillers at the end of the study (Figure 4.2). This relationship, however, was more pronounced for ungrazed plants (Figure 4.2), suggesting that grazing did hinder fescue tiller development.

Tiller dynamics through time, both within each growing season and between years, indicated several significant differences (Table 4.6). In particular, there was an overall year effect, as well as month*exclosure and month*covariate effects ($p < 0.05$). There was also a more complex four-way interaction between year*month*exclosure*grazing ($p < 0.05$; Table 4.6). All other interactions involving grazing were non-significant. To interpret the changes in tiller dynamics through time on each site and grazing treatment, yearly and monthly trends in tiller abundance are presented in Figure 4.3 for the Shirley and Tawayik exclosure locations (central LMU), and Figure 4.4 for the Ranger and Bailey locations (south LMU).

The number of tillers on both grazed and protected fescue plants at all exclosures decreased during the first month or two after transplantation, then stabilized throughout the rest of the growing season in 1999 (Figures 4.3 and 4.4). Initial declines were greatest on the Shirley (Figure 4.3A) and Ranger (Figure 4.4A) locations, with differences between exclosure locations carrying through until the end of the growing

season (Table 4.5). The initial declines in tiller numbers are evidence of stress imposed by transplantation, and may be a natural morphological and physiological response by the plant to divert photosynthates to fewer tillers to ensure survival of the plant itself (Bedunah and Sosebee 1995).

The use of standardized fescue transplantation techniques and randomized allocation of fescue cores to exclosure locations and grazing treatments suggests that the differences in tiller development among exclosure locations are due to either variation in growing conditions, or differences in the competitive nature of the pre-existing plant communities. While annual rainfall at each exclosure location was relatively similar in 1999 (Table 4.2), the distribution of rainfall over the growing season varied with location. The Shirley location received relatively little precipitation in the first two months after transplantation (46 mm). In contrast, approximately 65 mm of rain fell at the Tawayik and Bailey exclosure locations during this same time period. These data indicate that fescue cores at the Shirley location may have been more water stressed immediately following transplantation.

Given that the Ranger location received over 70 mm of precipitation in May and June of 1999, it is unlikely that moisture deficits account for the poor tiller development at this location. Examination of the species composition data (Table 4.4) shows that the Ranger site had the greatest abundance of Kentucky bluegrass. Kentucky bluegrass is an exotic, rapidly growing, rhizomatous grass that forms a sod when heavily grazed, and may limit rough fescue growth through competitive suppression (Bork 2000; Willoughby 1997; Trottier 1986). Similarly, shrub cover was generally greater at the Shirley location, and may have contributed to the poorer fescue establishment at that location (Table 4.4).

Additional variation in fescue morphological characteristics was evident among exclosures late in the growing season of 1999. In particular, fescue tiller counts began to increase on both grazed and protected plants at the Tawayik and Bailey exclosures (Figures 4.3A, 4.4A), as well as on ungrazed plants at the Ranger exclosure (Figure 4.4A).

Although limited overall grazing effects were observed on tiller counts in 1999 (Table 4.5), one prominent trend was evident, and likely accounts for the observed significant four-way interaction in Table 4.6: a marked difference in the number of tillers on grazed and ungrazed plants occurred at the Tawayik location (Figure 4.3A) with grazed plants having fewer tillers. This difference increased as the year progressed, and continued to widen during 2000 (Figure 4.3B). Utilization data (Figure 4.5) showed that grazed fescue plants at Tawayik received greater use than at any other location, and this may account for the increased grazing effect. Notably, fescue plants at all other exclosure locations remained well below an average of 50% utilization (Figure 4.5), which is often considered a maximum level of acceptable use for the grazing of fescue (Willoughby 1997; Trottier 1986; Willms et al. 1985).

Fescue tiller count data at Ranger followed the trends observed at the Tawayik location, although a grazing effect did not appear until August of 2000 (Figure 4.4B). This may be due to the lower level of utilization at this particular site (Figure 4.5), which would mean a longer period of defoliation stress was required before reductions in plant vigour occurred.

Two other grazing effects were evident within the tiller count data, but were limited to the second year of the study. At both the Shirley (Figure 4.3B) and Bailey

(Figure 4.4B) exclosure locations, grazed plants increased in tiller counts compared to protected plants during August and September of 2000. Although the cause of this difference is unknown, at the Shirley location it may be attributable to the increase in shrub cover on the protected grassland following construction of the exclosure. Protected and grazed areas at Shirley had a total live shrub cover of 65.1 and 27.4 %, respectively, by the end of 2000 (Table 4.2). Given that rough fescue tiller development is largely controlled by the amount of solar radiation available for photosynthesis (Willms et al. 1986), excessive shading may have limited tiller development at this location. Tiller development may also decline in the future within other exclosures where protection from herbivory increases shrub and tall herb cover (e.g., Ranger exclosure; Table 4.2) or litter accumulation, either of which may create less favourable conditions for tiller development. The increase in tillering outside the Shirley exclosure may also reflect the more open landscape in this region due to the occurrence of prescribed fire in 1989, 1991 and 1993. Fire has resulted in a more open landscape and increases alternative grazing opportunities for ungulates, which in turn, may facilitate fescue growth.

The cause of greater tiller development in grazed plants at the Bailey exclosure location in 2000 is unknown. However, the reduction in tiller numbers on the protected area may be at least partly due to protected fescue plants reallocating resources from tiller production to seed production (Figure 4.1). In addition, this exclosure is located on a sandy range site (Table 4.2), and has relatively low cover levels of other species, including shrubs and exotic herbs (Table 4.4). Consequently, plains rough fescue plants may simply be better adapted to the local site conditions at this location, regardless of

grazing pressure. Where grazing is removed, competition from other ungrazed herbs or an increase in litter may constrain tiller development.

4.6.3 Management Implications

These results indicate that while the elimination of grazing is not a prerequisite to the initial establishment of plains rough fescue in Elk Island National Park, grazing would have to be removed in order to maximize the success of fescue establishment (e.g., survival) in restoration projects. This is particularly likely given that future declines in vigour may lead to additional mortality of grazed plants. Although reductions in grazing pressure may also enhance fescue survival, this concept was not tested by this research. It is also possible, however, that moderate reductions in ungulate populations within the Park may not enhance fescue survival because of the limited primary rangeland (e.g., upland grasslands) available to grazing ruminants within the Park, and the intensive year-long grazing regime. To ensure the survival of transplanted rough fescue, ungulate spring and summer use would have to be reduced by either increasing the area of primary range within the Park, or markedly reducing ungulate numbers to levels below that at which fescue growth and survival declines.

Studies have indicated that bison, deer, and elk prefer grassland habitats during the spring and summer (Morgantini and Hudson 1989; Reynolds et al. 1978; Willms and McLean 1978). Since only 20% of Elk Island consists of this primary habitat (Jensen 2001), it is reasonable to assume that these areas experience heavy utilization during the growing season. Based on this assumption, stocking densities on upland grasslands within the Park during the growing season (May to September) are estimated to be 3.7

AUM/ha (based on 1999 ungulate populations; Table 4.1). In order to facilitate fescue recovery and/or re-establishment, the stocking density on upland grasslands within the Park would need to be reduced to below 1.2 AUM/ha, as indicated by other research in fescue grasslands (Willms et al. 1985). This would mean reducing bison herds to 330 animals, elk to 560, and maintaining the deer population at approximately 210 animals.

4.7 Conclusions

It has been suggested that intense ungulate herbivory in Elk Island over the last century has extirpated plains rough fescue from most of its natural habitat within the Park. Results of this study indicate that ungulate grazing negatively impacted the survival, growth, and development of transplanted plains rough fescue, although varying with exclosure location. To increase establishment, grazing should be removed or significantly reduced, especially since mortality may continue. This is supported by the reduction in fescue vigour (e.g., tiller counts) that occurred on grazed areas, which is likely to continue under present grazing conditions.

Ungrazed fescue plants are surviving well, particularly where initial competition from other plant species (e.g., exotic spp.) was low. This indicates that plains rough fescue can survive under these conditions, but may suffer should competition from exotic species (e.g., Kentucky bluegrass) and shrubs increase. In this case, burning and periodic herbivory may be beneficial in controlling the expansion of woody and invasive species, respectively. The notable variation in response of plains rough fescue at different exclosures over the two years of the study may be indicative of either variation in growing conditions (e.g., summer precipitation), grazing pressure, plant community

composition, or ecosite conditions at each location. Regardless of the mechanism, this variation suggests that intensive restoration efforts of plains rough fescue in EINP will be difficult.

4.8 Literature Cited

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Table 4.1: Approximate ungulate populations in the Main Park and Isolation Area of EINP for the period 1910 to 1999 [values compiled from Blyth (1995) and Parks Canada (1999)].

Ungulate species	1910	1920	1930	1940	1950	1960	1970	1980	1990	1999
Main Park (13600 ha)										
Moose	19	70	400	113	272	83	280	380	231	250
Elk	30	200	467	473	800	154	350	500	872	1450
Plains Bison	45	200	716	995	1350	750	831	421	444	638
Mule Deer	30	150	200	27	150	0	-	-	-	-
Whitetail Deer	-	-	-	-	1	90	74	120	201	150
Isolation Area (5800 ha)										
Moose	-	-	-	-	-	80	225	100	77	90
Elk	-	-	-	-	-	90	25	75	320	420
Plains Bison	-	-	-	-	75	236	0	-	-	-
Wood Bison	-	-	-	-	-	-	32	110	232	405
Whitetail Deer	-	-	-	-	-	155	265	130	65	60
Total (19400 ha)	124	620	1783	1608	2648	1638	2082	1836	2442	3463*

* Equivalent to a year-long stocking rate of about 2.0 AUM/ha throughout the Park.

Table 4.2: Summary ecosite and vegetation overstory descriptions for protected and grazed grassland communities at each of the four exclosure locations investigated.

Exclosure Location	Grazing Treatment	Slope (%)	Aspect	1999 Rainfall (mm)	2000 Rainfall (mm)	Soil Texture*	2000 Shrub Cover (%)
Ranger	protected	18	SE	180	208	SL	38.1
	grazed	14	SE			L	<5**
Shirley	protected	10	SW	172	175	C	65.4
	grazed	11	S			CL	27.7
Tawayik	protected	8	S	193	227	L	9.3
	grazed	10	SE			L	5.2
Bailey	protected	5	NW	187	198	S	15.3
	grazed	0	n/a			S	18.4

* C = clay, L = loam, S = Sand.

** While shrub cover was not measured in the plant community where fescue was transplanted, visual reconnaissance indicated that shrubs on the transplant site were sparse. This number is a generous estimation of shrub cover on that site.

Table 4.3: Exclosure location and grazing effects on survival and morphological characteristics [means ± (SE)] of live plains rough fescue within each plant community in August 2000.

Anova	df	Percent Survival		Basal Diameter (cm)		Fescue Height[a] (cm)	
		F	P	F	P	F	P
Exclosure Location (E)	3	1.00	0.500	5.13	0.106	1.07	0.478
Ranger		95 (5)		1.6 (0.2)		28.1 (1.6)	
Shirley		90 (10)		2.3 (0.3)		10.9 (1.1)	
Tawayik		95 (5)		3.1 (0.3)		30.5 (2.0)	
Bailey		90 (10)		2.6 (0.3)		13.8 (1.2)	
Grazing (G)	1	27.00	**0.014**	17.85	**0.024**	36.25	**0.009**[#]
Protected		100 (0)a		3.2 (0.2)a		21.2 (1.5)	
Grazed		85 (3)b		1.6 (0.2)b		20.5 (1.8)	
E x G*	3	n/a	n/a	1.32	0.274	2.34	0.081
Ranger Protected				2.2 (0.3)		30.1 (2.7)	
Ranger Grazed				0.9 (0.3)		11.4 (2.1)	
Shirley Protected				3.2 (0.4)		27.6 (1.6)	
Shirley Grazed				1.5 (0.3)		15.6 (1.6)	
Tawayik Protected				4.2 (0.5)		26.1 (1.7)	
Tawayik Grazed				2.0 (0.2)		10.4 (0.6)	
Bailey Protected				3.1 (0.5)		33.4 (3.7)	
Bailey Grazed				2.0 (0.2)		12.0 (1.4)	
Error**	71						

[a] Data transformed prior to analysis using square root transformation; original data presented for clarity.

[#] Statistical analysis of transformed data showed significant differences not illustrated by original data.

* Error term for tests of exclosure location and grazing effects.

** Error term to test interaction effect.

Note: Within each morphological characteristic and treatment combination means with different lower case letters differ significantly (p<0.10).

Table 4.4: Percent cover of major plant species (minimum 1% cover) found in each grassland plant community investigated in 2000.

Plant Species	Ranger Protected	Ranger Grazed*	Shirley Protected	Shirley Grazed	Tawayik Protected	Tawayik Grazed	Bailey Protected	Bailey Grazed
Grasses:								
Agropyron spp.	<1	<1	<1	1.5	-	<1	<1	<1
Carex spp.	<1	-	1.1	<1	<1	<1	6.5	3.5
***Festuca hallii* (Vasey) Piper**	-	-	-	-	-	-	<1	-
Festuca saximontana Rydb.	-	-	-	-	-	-	<1	<1
Poa pratensis L.	21.9	14.9	2.9	19.1	4.2	21.6	<1	1.9
Phleum pratense L.	<1	<1	1.1	<1	1.9	2.6	-	-
Schizachne purpurascens (Torr.) Swallen	1.9	<1	1.1	-	-	-	<1	1.1
Total Grasses	26.8	17.9	7.2	22.6	7.1	26.2	11.5	8.5
Forbs:								
Achillea millefolium L.	1.5	<1	2.9	4.9	6.4	2.8	2.6	5.3
Aster spp.	<1	<1	1.0	2.1	<1	<1	2.6	<1
Fragaria virginiana Duchesne	2.8	3.9	19.6	8.8	<1	<1	1.4	1.4
Galium boreale L.	2.6	1.3	3.2	<1	<1	1.3	1.8	<1
Plantago major L.	<1	<1	-	-	3.3	3.0	-	-
Solidago canadensis L.	1.8	1.1	<1	-	-	-	-	-
Taraxacum officinale Weber	11.2	4.0	<1	<1	18.9	11.6	-	-
Trifolium spp.	1.9	8.3	1.5	6.3	20.4	52.4	1.6	<1
Vicia americana Muhl.	<1	-	1.3	1.6	1.2	1.0	1.5	1.1
Total Forbs	24.8	21.6	31.5	25.7	53.2	74.1	11.5	10.8
Shrubs:								
Amelanchier alnifolia Nutt.	1.1	<1	1.9	2.3	-	-	<1	4.3
Populus tremuloides Michx.	-	<1	-	-	3.1	-	6.9	3.6
Prunus virginiana L.	1.1	<1	24.8	8.5	-	-	-	-
Rosa woodsii Lindl.	5.3	18.8	11.0	7.4	-	-	-	<1
Rubus idaeus L.	4.8	15.7	4.7	<1	-	-	-	-
Symphoricarpos occidentalis Hook.	25.8	16.3	22.7	8.2	5.3	4.2	2.7	<1
Vaccinium myrtilloides Michx.	-	-	-	-	-	-	4.3	4.0
Total Shrubs	38.1	53.8	65.1	27.4	8.4	4.2	14.9	13.9
Litter Cover	25.3	35.3	85.6	45.0	46.3	25.6	26.1	25.0

* Cover values for this site were not available. Values presented in this table are from a plant community with much higher shrub cover than that where the fescue was transplanted.

Table 4.5: Effect of exclosure location and grazing treatments on September live tiller counts [mean ± (SE)] for 1999 and 2000, analyzed using May tiller counts of each year as covariates for their respective years.

Anova		Tillers per Plant[a]	
		1999	2000
Exclosure Location (E)	3	$F = 16.45$**	$F = 1.00$
Ranger		13 (2)a	17 (3)
Shirley		7 (1)a	9 (4)
Tawayik		24 (3)b	32 (4)
Bailey		26 (3)b	28 (4)
Grazing (G)	1	$F = 3.24$	$F = 0.05$
Protected		20 (2)	24 (3)
Grazed		15 (2)	19 (3)
Covariate	1	$F = 20.93$***	$F = 38.64$***
E x G	3	$F = 1.16$	$F = 1.42$
Error	71		

[a] data transformed prior to analysis using the square root transformation; original data presented for clarity.
, * indicate $p<0.05$ and $p<0.01$, respectively.
Note: Within each year and treatment combination means with different lower case letters differ significantly $(p<0.10)$.

Table 4.6: Effect of grazing treatment and exclosure location on 1999 and 2000 live fescue tiller counts over time using repeated measures analysis (Wilk's Lambda Statistic).

Anova	df	F value	P value*
Year	1	4.2153	**0.0441**
Year*Exclosure	3	1.0386	0.3815
Year*Grazing	1	0.1596	0.6909
Year*Covariate	1	1.3387	0.2515
Year*Exclosure*Grazing	3	1.0457	0.3784
Month	3	2.1625	0.1012
Month*Exclosure	9	2.5960	**0.0082**
Month*Grazing	3	1.1414	0.3393
Month*Covariate	3	3.0652	**0.0343**
Month*Exclosure*Grazing	9	1.0603	0.3953
Year*Month	3	1.2428	0.3017
Year*Month*Exclosure	9	1.5918	0.1222
Year*Month*Grazing	3	0.5630	0.6414
Year*Month*Covariate	3	1.7781	0.1604
Year*Month*Exclosure*Grazing	9	2.2486	**0.0217**

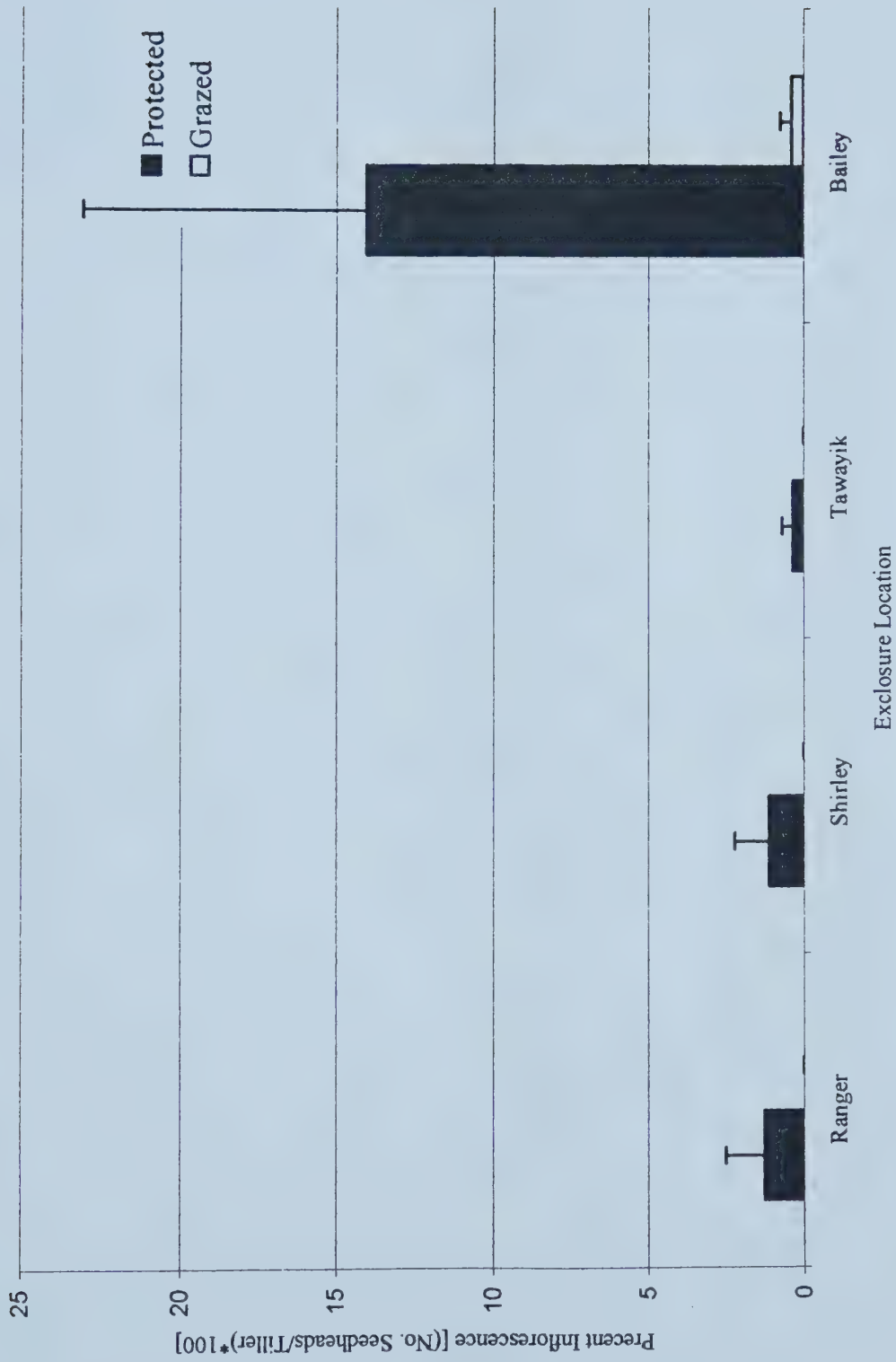* Bolded p-values indicate significant time effects $(p<0.05)$.

Figure 4.1: Percent reproductive tillers of *Festuca hallii* plants in 2000 (means and SEs).
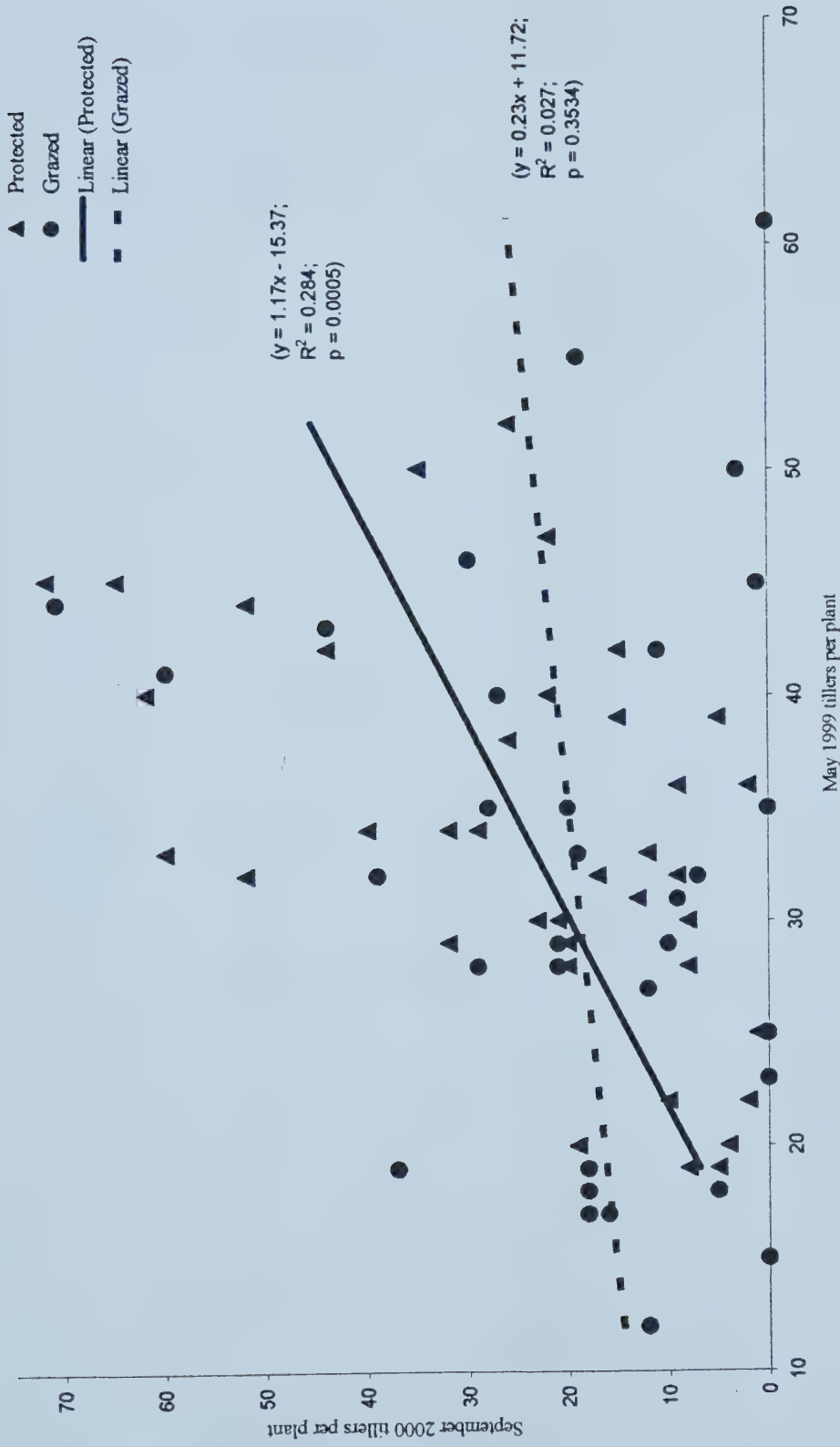
Figure 4.2: Correlation of final tillers per plant (September 2000) with initial tiller counts per plant (May 1999).
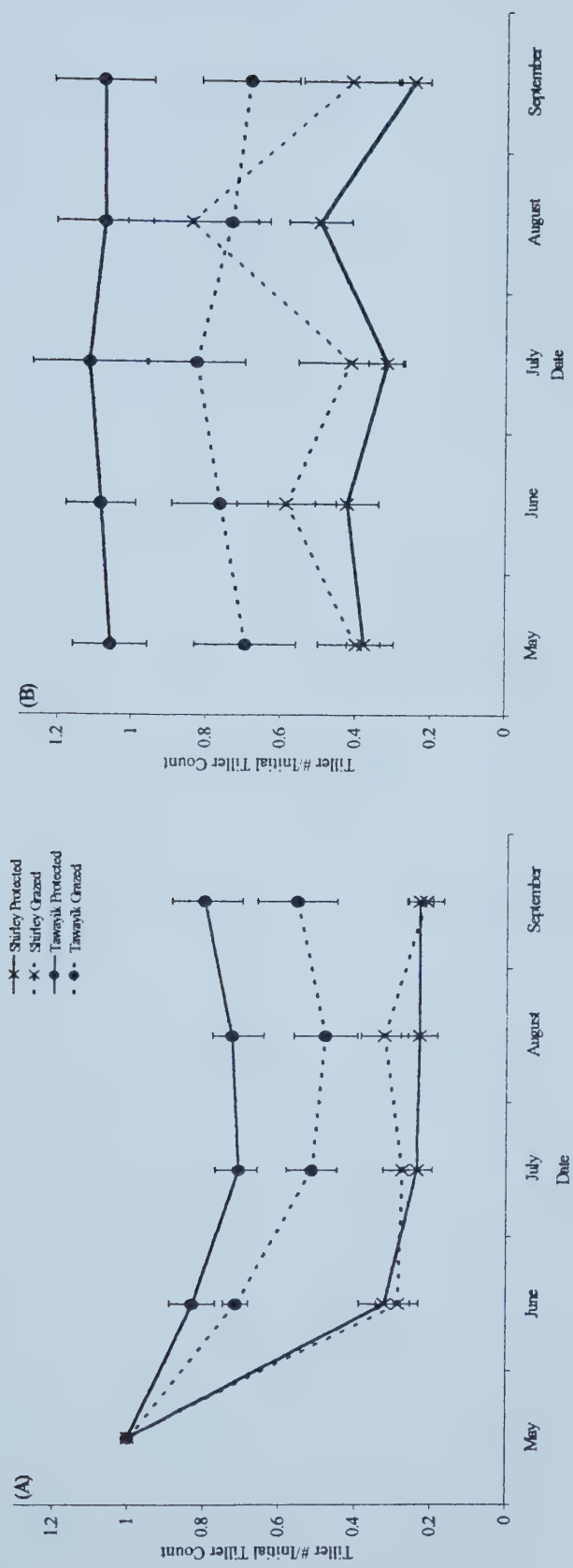
Figure 4.3: Changes in fescue tiller numbers on grazed and protected sites in the Main Park of EINP in 1999 (A) and 2000 (B).
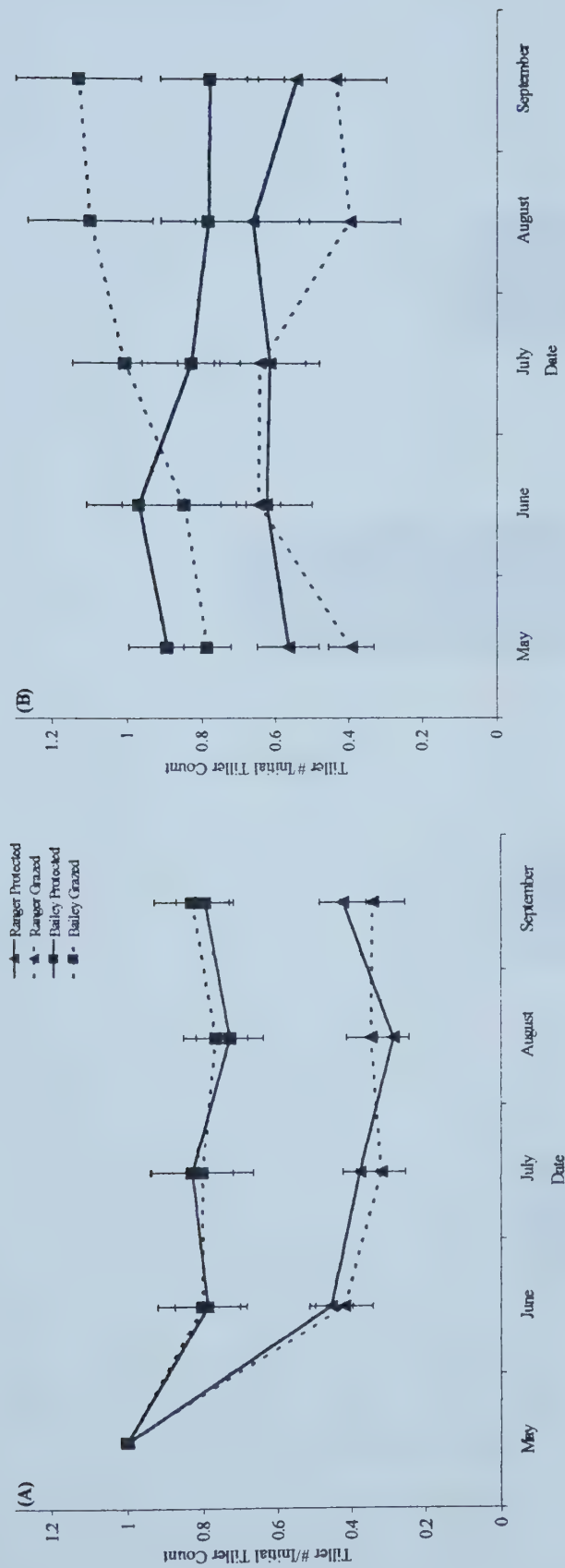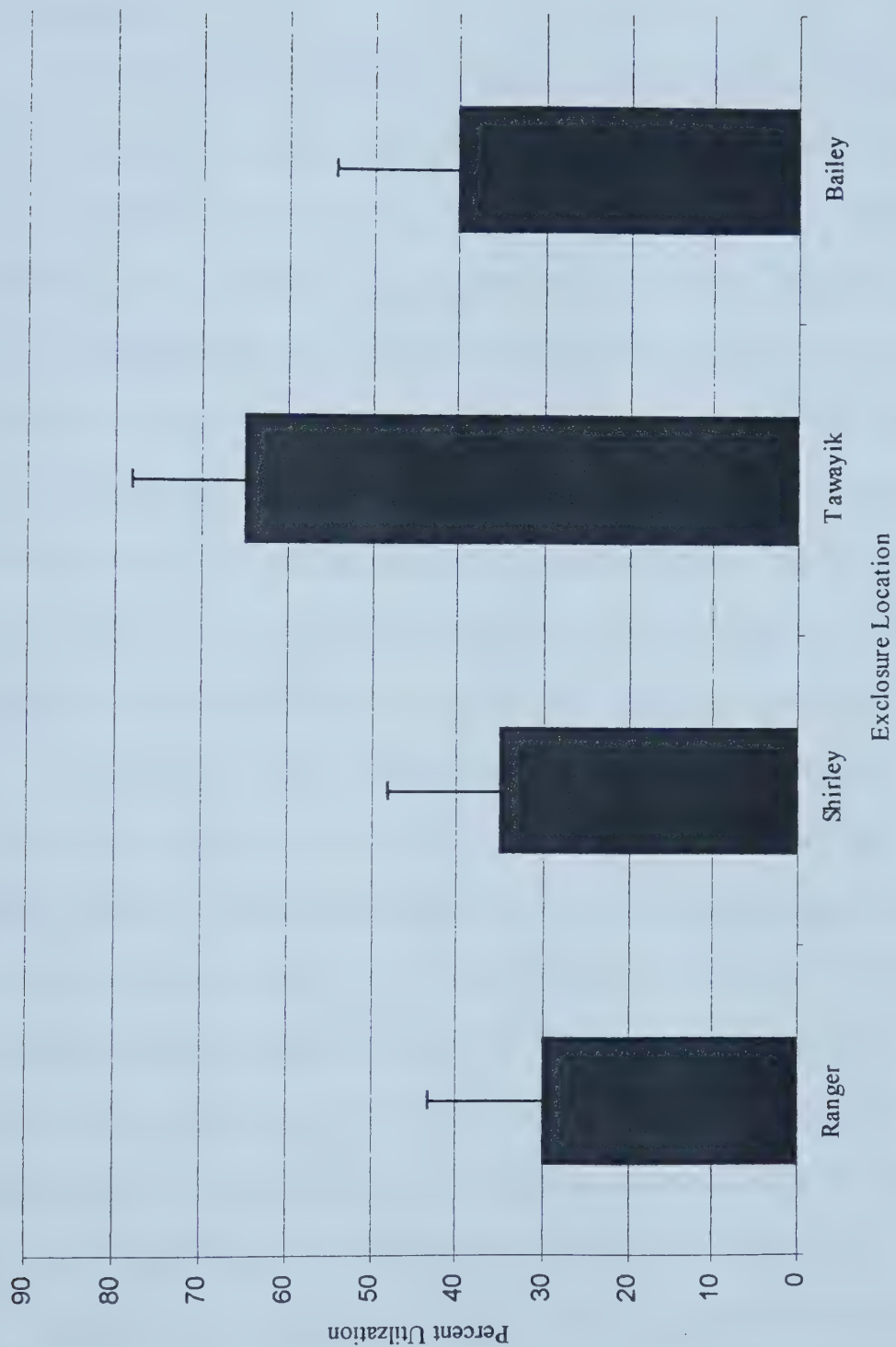
Figure 4.4: Changes in fescue tiller numbers on grazed and protected sites in the Isolation Area of EINP in 1999 (A) and 2000 (B).

Figure 4.5: Percent utilization of fescue tillers in September 2000 (means and SEs).

CHAPTER 5: *Corylus cornuta* **Marsh. Resilience to Herbivory in Elk Island National Park.**

5.1 Introduction

Elk Island National Park (EINP) is located in east-central Alberta, and has an understory dominated by dense stands of beaked hazel (Hardy et al. 1986; Polster and Watson 1979). Prescribed fire and herbivory are two of the main factors affecting vegetation within the Park (Parks Canada 1999; Bork et al. 1997a). Specifically, intense year-long herbivory over the past 80 years has resulted in reduced aspen regeneration and a reduction in preferred browse species such as chokecherry (*Prunus virginiana* L.), saskatoon (*Amelanchier alnifolia* Nutt.), and red-osier dogwood (*Cornus stolonifera* Michx.) (Parks Canada 1999; Bork et al. 1997a, 1997b; Blyth et al. 1993; Polster and Watson 1979; Milner 1977). In contrast, beaked hazel has increased in abundance and comprises 62% of available browse within the Main Park (Blyth et al. 1993).

Beaked hazel (*Corylus cornuta* Marsh.) is a common understory shrub within the Lower Boreal Mixedwood (LBM) forest of Alberta (Strong and Leggat 1982). Beaked hazel occurs mainly in the east-central portion of the LBM within the province, on moderately well-drained, moist sites (Willoughby et al. 1997). Beaked hazel is an important understory species with the potential to influence forest ecology. High hazel densities can inhibit tree reproduction and reduce the abundance of more palatable browse species, as well as change the light intensity available to understory herbaceous plants and affect the chemical composition of litter (Tappeiner 1979, 1971).

Beaked hazel is a prolific shrub with the ability to produce clones by way of underground stems, which in turn produce new roots and aerial stems along their length

(Tappeiner and John 1973). While it is commonly believed that this is the main method of reproduction, Tappeiner (1971) observed that more than 46% of beaked hazel clones in northern Minnesota were only 30 cm in diameter and all clones were less than 2 metres across, with most of the reproduction actually by seed. As stands of hazel age, the total phytomass and proportion of young stems in the population generally increases. However, as a tree overstory develops and shade increases, hazel density eventually declines (Kurmis and Sucoff 1989).

Management of beaked hazel has often examined methods to control its density through herbicides and prescribed fire. Several studies report that hazel is susceptible to fire, with mortality of above-ground biomass accomplished at various fire intensities (Johnston and Woodard 1985; Tappeiner 1979). Failure to kill below-ground hazel biomass, however, resulted in vigorous resprouting of stems and increased hazel density (Tappeiner 1979). In contrast, herbicides can be effective in achieving up to 98% mortality of hazel plants (Tappeiner 1979), allowing less competitive shrubs to increase.

Despite the abundance of beaked hazel in EINP and its key role in providing abundant browse to native ungulates, there remains little information on the intra-specific response of this ubiquitous shrub to current levels of herbivory within the Park. Given that mortality of aerial hazel stems has previously been found to increase stem density (Tappeiner 1979), heavy browsing within the Park may be significantly increasing hazel current annual production, rather than decreasing it. Given the importance of this shrub to the survival of browsing ungulates in EINP, a study was designed to assess the effect of current browsing on beaked hazel shrubs, either positive or negative. To accomplish this, the morphological and production responses of shrubs protected in newly established

ungulate exclosures were compared with those in adjacent communities exposed to year-long herbivory. The null hypothesis was that browsing does not affect hazel twig morphology or twig and leaf current annual production.

5.2 Study Area

Elk Island National Park is a 194 km² area situated 37 km east of Edmonton, Alberta (53°37'N, 112°58'W) within the Beaver Hills-Cooking Lake Moraine. The Park is elevated between 30 and 60 m above the surrounding plains (710 to 760 m ASL), and is composed of knob and kettle topography, with slopes approximately 0 to 20%. Upland soils are mostly well-drained Orthic Gray Luvisols under forest (Crown 1977), while Dark Gray Luvisols occupy more open areas. Soil textures vary from loam to silty loam or loamy sand. Soil textures vary from loam to silty loam or loamy sand.

Located in the cool continental, sub-humid climatic region, EINP receives about 450 mm of precipitation annually, with 75% falling as summer rain (Environment Canada 1993). Temperatures vary from -40°C in winter to 32°C in summer.

Uplands are mostly dominated by aspen (*Populus tremuloides* Michx.) forest, which covers roughly 80% of the Park. The understory consists of a variety of herbs and shrubs, of which marsh reedgrass (*Calamagrostis canadensis* (Michx.) Beauv.), and beaked hazel are the most abundant (Bork et al. 1997a). South-facing slopes and drier sites are dominated by grasslands of primarily introduced plant species including Kentucky bluegrass (*Poa pratensis* L.) and dandelion (*Taraxacum officinale* Weber).

Elk Island is the only fenced national park in Canada. Substantial ungulate populations are found in the Park, and place great demand on the vegetation all year, as

animal migration is restricted by the 2.2 m perimeter fence. In 1999, roughly 640 plains

bison (*Bison bison*), 400 wood bison (*Bison athabascae*), 340 moose (*Alces alces*), 1850

elk (*Cervus elaphus*), and fluctuating whitetail and mule deer populations (*Odocoilius*

virginianus and *O. hemionus*) were supported by the habitat in EINP (Parks Canada

1999). Given that this study is concerned with the effect of browsing on beaked hazel, a

major source of winter forage within the Park, it is important to note that these year-long

stocking densities (Table 5.1) are among the highest in North America.

As a result of a management workshop held in 1997, the Park was

administratively divided into three land management units (LMU) to facilitate ecological

monitoring and management (Equus Consulting Inc. 1997). The south LMU is located

south of Highway 16, and is physically separate from the Main Park. The central and

northern LMUs are north of Highway 16. Within each LMU, four long-term bio-

monitoring plots (LTBP) (0.5 by 2 km) have been established for monitoring Elk Island's

natural resources (Cool 1999).

5.3 Experimental Design

In the fall of 1998, four ungulate proof exclosures, each 20 by 50 m in size, were

constructed in EINP. These exclosures were distributed throughout the Main Park with

two in each of the north and central LMUs. In addition, each exclosure was located

within a LTBP to complement current bio-monitoring programs. Exclosure fences were

2.2 m tall to exclude all ungulates.

Exclosure locations were randomly selected within each LTBP, although each

exclosure was positioned locally to include a forest community type with a beaked hazel

understory. Plot pairs consisted of an aspen-hazel plant community divided by the exclosure fence, initially resulting in two areas of similar plant species composition and structure, as well as ecosite characteristics at each exclosure (Table 5.2). Aspen-hazel communities outside the exclosure were exposed to continuous year-long native ungulate browsing, while protected plant communities were allowed to recover following the cessation of ungulate herbivory in October of 1998.

In this investigation, plant communities were considered the experimental unit at each exclosure, with the latter treated as blocks. This was done because sub-sampled hazel stems were constrained by plant community at each exclosure, which violated the assumption of complete randomization (Hurlbert 1984).

5.4 Vegetation Sampling

In each forested plant community inside and outside each exclosure, 20 beaked hazel shrubs were randomly sampled in August of 1999 and 2000, the first and second years following exclosure construction, to represent the larger population of shrubs in each area. A single, 15 m transect was established in each plant community, with two beaked hazel shrubs randomly selected and tagged at each of 20 sample points at 0.75 m intervals along each transect (total = 40 shrubs per plant community). Individual shrubs were defined as free-standing stems at the soil surface. All stems were less than 2.5 m tall. In each year, one of the shrubs at every interval was sampled, resulting in 20 shrubs measured inside and 20 outside at each of the four exclosures in 1999 (N=160), with another 160 shrubs sampled in 2000. Parameters measured on each shrub included the number of current annual growth (CAG) twigs per shrub, the total length of CAG twigs,

together with the mass of CAG twigs and leaves. Phytomass was assessed by clipping all CAG, oven drying clippings at 50°C for 48 hours, and weighing each sample to determine twig and leaf CAG per plant. Clippings were later pooled by plant community and analyzed for crude protein (CP) and acid detergent fibre (ADF). Crude protein analysis was done using a Nitrogen Determinator (LECO Corporation, St. Joseph, MI, USA). ADF was measured using the filter bag technique described by ANKOM Company (1993).

Two additional 15 m transects were located in each plant community to measure overstory tree canopy cover, hazel cover, total shrub density, hazel density, and hazel CAG per unit area during peak growth of 2000. Tree canopy cover was estimated along each of the two transects using the line intercept method (Bonham 1989). In addition, tree density was measured in a 20 by 20 metre area. Hazel cover (ocular estimation - Daubenmire 1959), total shrub density, and hazel density were sampled at two metre intervals along both transects within 1 m^2 quadrats (N = 16). Woody plants less than 2.5 m tall were considered shrubs. Plant community hazel CAG (per unit area) was measured from 0.25 m^2 clipped quadrats placed at the 5 and 11 metre locations along each transect. Hazel CAG per unit area was oven-dried at 50°C for 48 hours, then weighed. Data were again pooled to give a mean value per plant community, the latter of which was treated as the experimental unit.

Within each plant community, ecosite data was collected on slope gradient, aspect, precipitation and soils (Table 5.2). Soil cores were collected in October 2000 and analysed for soil texture using the hydrometer method described by McKeague (1978).

5.5 Data Analysis

All data were checked for normality and homogeneity using the Shapiro-Wilkes statistic prior to analysis. Data that were not normal or homogenous were transformed. Hazel cover and production per unit area, as well as all CAG parameters measured on individual shrubs were log-transformed, while hazel shrub density was square-root transformed.

Total shrub density and hazel cover, density, and production per unit area were analysed using a randomized complete block design (Steel et al. 1997). Exclosure location and browsing effects were analysed using their interaction as the error term. Individual shrub CAG parameters were similarly analyzed using a randomized complete block design. However, in addition to testing for exclosure location and browsing effects, the interaction was tested using the error provided by variation among individual hazel shrubs. An alpha level of $p<0.10$ was used to determine significan effects. Post-hoc mean comparisons were conducted on all significant variables using Tukey's test ($p<0.10$).

5.6 Results & Discussion

5.6.1 Plant Community Responses

Total shrub density, as well as hazel density, cover, and current annual growth (CAG) per unit area varied among exclosure locations ($p<0.10$), but were similar among browsing treatments in 2000 (Table 5.3). Among the four locations, Astotin had the most dense and productive beaked hazel population, followed by the Shirley, Boreal, and

Tawayik exclosures, respectively. Variation in plant community characteristics is likely attributable to differences in ecosite conditions (Table 5.2), which contribute to the composition and productivity of the shrub layer. Beaked hazel generally prefers more open, mesic sites (Willoughby et al. 2000; Buckman 1964).

Although greater CAG at the Astotin location may be partly the result of increased summer rainfall at this location during the two years of the study (Table 5.2), favourable precipitation should not account for the increase in density of a perennial species such as hazel. Instead, the abundance of hazel at the Astotin site may be the result of a relatively open tree canopy (Table 5.2), which would help maintain high densities of hazel (Kurmis and Sucoff 1989).

At least one other location (Tawayik) had a similar precipitation level, but markedly less hazel (Table 5.3). The latter site, however, included a well-developed, closed forest canopy (Table 5.2), indicating that light, rather than moisture, probably regulates hazel stem densities within the communities investigated. Regardless of the cause, the differential densities of beaked hazel among sites likely plays an important ecological role by influencing other plants through interspecific competition (Lauer and Glover 1999), as well as its own population through intense intraspecific competition (e.g., at the Astotin site), a phenomenon also documented by Bedunah and Sosebee (1995).

Of the four sites examined, only one had been exposed to fire during the last decade. The Shirley site was burned in the spring of 1989, 1991 and 1993. Despite those fires, hazel continues to have a major presence in the understory at this site (Table 5.3). Other research supports the notion that beaked hazel is relatively well-adapted to fire,

particularly episodic fire (Johnston and Woodard 1985; Tappeiner 1979), with frequent annual summer fires needed to eliminate hazel (Buckman 1964).

At the plant community level, only one difference was observed between vegetation recently protected from browsing and that still exposed to ungulates: maximum shrub height increased by nearly 50% within the exclosures following release from annual year-long browsing ($p<0.01$; Table 5.3). In contrast, hazel cover, density, and CAG per unit area remained similar between browsed and protected communities.

5.6.2 Hazel Morphological & CAG Responses

Individual hazel stem morphological and CAG parameters varied significantly with the exclosure location*browsing interaction effect ($p<0.05$) in both 1999 and 2000 (Table 5.4). Trends for morphological and production characteristics are illustrated in Figures 5.1 and 5.2, respectively, by exclosure location and browsing treatments.

Beaked hazel stems at the four exclosures differed in their specific responses to the removal of browsing. For instance, little difference was observed between protected and browsed hazel shrubs at the Shirley location in either the number of CAG twigs produced or their total length (Figure 5.1), nor the CAG of twig or leaf biomass (Figure 5.2). The lack of differences persisted over both years of the study, and may be due to the burn history of the area. Fire could have limited potential hazel response following exclosure establishment in 1998 by reducing the *a-priori* vigor of those shrubs remaining on the site. This is unlikely, however, given that the last fire occurred five years prior to exclosure establishment and the fire-adapted nature of beaked hazel. A more likely explanation is a generalized reduction in ungulate herbivory outside the exclosure.

Repeated prescribed burning has opened up the landscape in the area surrounding this exclosure such that less than 20% of the upland landscape is forested. This overall change in vegetation may be influencing browsing activities, particularly during the winter when adjacent forest cover is necessary for ungulates to cope with cold temperatures.

In addition to burning, physical site characteristics such as slope, aspect, and soil texture differentiate the Shirley location from others (Table 5.2). Steeper slopes with northwestern aspects indicate that beaked hazel communities at this location may experience cooler microclimates, resulting in less hazel production.

Unlike the Shirley site, the other three all showed differences between browsed and unbrowsed hazel plants. At the Tawayik exclosure location, hazel shrubs protected from browsing showed either little response to the removal of browsing or even a slight reduction in growth in 1999 (Figure 5.2C), but displayed a marked increase in growth one year later during 2000. Total CAG twig length was greater on a per shrub basis (Figure 5.1B), while the CAG of both leaf and twig phytomass were greater on hazel shrubs protected from browsing (Figures 5.2B and 5.2D). A similar response was observed at the Boreal exclosure location, but included a more pronounced decrease during 1999 in the number and length of twigs (Figures 5.1A and 5.1C) and phytomass (Figures 5.2A and 5.2C), followed by a sharp increase in growth the following year. The final location (Astotin) contrasted with the others, as rested hazel shrubs displayed the exact opposite pattern, slightly increasing growth during 1999 immediately following exclosure construction. Notably, no difference in either twig length or number (Figure 5.1), or twig

or leaf phytomass (Figure 5.2) were observed between browsed and unbrowsed hazel stems one year later at the Astotin exclosure.

The delayed response of hazel shrubs to the removal of browsing may be indicative of very intense levels of defoliation prior to exclosure establishment, which would have weakened shrubs by reducing photosynthetic capacity, plant carbohydrates and overall plant vigour (Bedunah and Sosebee 1995). The immediate decrease in hazel CAG at the Tawayik and Boreal exclosure locations (Figures 5.1 and 5.2) suggests that in the short-term (year to year), browsing may stimulate plant growth as hazel shrubs actively regrow to maintain sufficient photosynthetic area to survive. Immediately following the removal of browsing during the winter of 1998-99, these shrubs may have reduced above-ground growth the following summer because previous year CAG did not need to be replaced, allowing more energy (e.g., photosynthates) to be allocated to developing roots. As much as 31 to 39 % of hazel biomass is below-ground (Tappeiner and John 1973), and plays a key role in determining hazel survival.

Nevertheless, the marked increase in hazel production at these two locations one year later in 2000 (Figures 5.1 and 5.2) indicates that in the longer-term, browsing appears to reduce individual beaked hazel stem productivity. After one full year's rest, protected hazel shrubs were larger and probably had better developed root systems than their browsed counterparts, which would allow them to allocate more resources to above-ground growth in the second year of the study.

The limited response of beaked hazel stems at the Astotin exclosure location may be attributable to several factors, including precipitation, overstory cover, browsing pressure, and intraspecific competition. The high amount of summer rainfall and open

tree canopy at this location may allow beaked hazel shrubs to more easily tolerate defoliation. In addition, while shrubs at Astotin are clearly browsed (as evidenced by a visible browse-line; Figure 5.3), they are larger than shrubs at other locations (Table 5.3) and may be more developed, allowing them to better tolerate intense herbivory. Perhaps the most important factor influencing the response of individual hazel shrubs at the Astotin location is the high hazel density and canopy cover. Beaked hazel plants have been shown to compete very effectively with other shrub species by reducing the intensity of light reaching the forest floor (Tappeiner 1979; Tappeiner and Alm 1975; Tappeiner and John 1973). The results found here suggest that hazel stems also compete with each other for resources and may struggle to maintain growth at high stand densities, negating any potential effects of removing herbivory.

5.6.3 Hazel Browse Quality

Overall, there were relatively few significant impacts on the quality of hazel browse, with more effects apparent as a result of site differences than browsing. For example, twig and leaf crude protein levels in 2000 differed among the exclosure locations ($p<0.05$), with the Boreal location having lower levels of twig protein than the others (Table 5.5). In contrast, leaf crude protein was lower for the Shirley exclosure location, but greater for Tawayik, relative to the others (Table 5.5). These differences likely reflect unique total hazel phytomass levels at each site, along with differences in growing conditions and soil parameters.

Only one nutritional variable displayed a significant interaction between exclosure and browsing ($p<0.01$), that being leaf crude protein (Table 5.5). At two locations

(Boreal and Shirley), leaf protein was greater for browsed hazel shrubs in 2000.

Examination of the phytomass data in Figure 5.2D indicates that the increase in browse

quality ourtside the Boreal exclosure coincides with a reduction in leaf phytomass. This

response exemplifies the typical inverse relationship often found between forage quantity

and quality, with an increase in one reducing the other (Van der Wal et al. 1999; Clark et

al. 1998; Coppedge and Shaw 1998; Cid and Brizuela 1998). The increase in protein at

the Shirley exclosure, however, does not follow this pattern. Instead, leaf phytomass is

similar between browsed and unbrowsed shrubs (Figure 5.2d), indicating the increase in

hazel leaf protein concentration within the exclosure (Table 5.5) may be additive,

increasing total standing leaf protein phytomass (e.g., crude protein yield) of hazel. This

response may reflect the recent burn history of this site. Cessation of browsing may

allow beaked hazel to grow to a greater extent, both above and below-ground, potentially

increasing its ability to capture nutrients released by recent fires, either through

combustion or mortality of plants and subsequent root necrosis and decomposition.

Given the prevalence of hazel in the Park and its importance for herbivores, as well as the

extensive use of prescribed fire by Park managers, this relationship may merit further

investigation.

5.6.4 Management Implications

The favourable response of individual hazel shrubs to the removal of browsing

suggests that although browsing appears to have increased beaked hazel in the past

(especially with the decline of other, more palatable shrubs), herbivory does reduce

beaked hazel production in the long-term. To ensure continued vigour and production of

beaked hazel as a key forage species, ungulate populations may have to be reduced to levels that are not detrimental to hazel shrubs, although the extent to which browsing pressure may have to be changed remains untested. This is particularly likely if burning, by removing forest and converting woodlands into grasslands, continues to reduce hazel distribution and abundance in the Park, placing greater browsing pressure on the remaining hazel. Hazel stems are very susceptible to late season fire (Johnston and Woodard 1985), with multiple fires capable of killing underground stems and preventing resprouting (Johnston and Woodard 1985; Buckman 1964). Thus, further research is needed on how fire and specific utilization levels (e.g., ungulate stocking rates) impact hazel before more specific recommendations can be made.

5.7 Conclusion

Other than through structural changes, beaked hazel plant community characteristics do not generally appear to be detrimentally affected by browsing in the short-term. The response of individual beaked hazel shrubs to the removal of herbivory, however, depended heavily on sampling location throughout Elk Island National Park. The lack of beaked hazel response at some exclosure locations (e.g., Astotin and Shirley) may indicate that other factors such as precipitation, micro-climate, competition, overstory characteristics, and previous management (e.g., fire) play a major role in beaked hazel production. At other locations (e.g., Boreal and Tawayik), hazel shrub responses supported an alternate hypothesis that browsing increases hazel production in the short-term, but reduces the production of hazel in the longer-term relative to the

unbrowsed state. These results have implications for *Corylus cornuta* and ungulate

management within EINP.

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Table 5.1: Approximate ungulate populations in the Main Park and Isolation Areas of EINP for the period 1910 to 1999 [values compiled from Blyth (1995) and Parks Canada (1999)].

Area & Ungulate species	1910	1920	1930	1940	1950	1960	1970	1980	1990	1999
Main Park (13600 ha)										
Moose	19	70	400	113	272	83	280	380	231	250
Elk	30	200	467	473	800	154	350	500	872	1450
Plains Bison	45	200	716	995	1350	750	831	421	444	638
Mule Deer	30	150	200	27	150	0	-	-	-	-
Whitetail Deer	-	-	-	-	1	90	74	120	201	150
Isolation Area (5800 ha)										
Moose	-	-	-	-	-	80	225	100	77	90
Elk	-	-	-	-	-	90	25	75	320	420
Plains Bison	-	-	-	-	75	236	0	-	-	-
Wood Bison	-	-	-	-	-	-	32	110	232	405
Whitetail Deer	-	-	-	-	-	155	265	130	65	60
Total (19400 ha)	124	620	1783	1608	2648	1638	2082	1836	2442	3463*

* Equivalent to a year-long stocking rate of 2.0 AUM/ha throughout the Park.

Table 5.2: Summary ecosite descriptions for protected and browsed forest communities at each of the four exclosures investigated.

Exclosure Location	Browsing Treatment	Slope (%)	Aspect	1999 Rainfall (mm)	2000 Rainfall (mm)	Soil Texture	Tree Density (#/400m^2)	Tree Cover (%)
Boreal	protected	16	NE	141	178	L to SL	56	76
Boreal	browsed	19	N	141	178	SL	54	82
Astotin	protected	13	SW	330	264	L	11	7
Astotin	browsed	13	W	330	264	L	4	11
Shirley	protected	27	NW	172	175	C	37	55
Shirley	browsed	20	NW	172	175	CL	20	30
Tawayik	protected	0	n/a	193	227	L	79	66
Tawayik	browsed	0	n/a	193	227	L to SL	78	82

L = loam, SL = sandy loam, C = clay, CL = clay loam.

Table 5.3: Exclosure location and browsing effects on beaked hazel characteristics [mean ± (SE)] within each plant community in 2000.

Anova	df	Hazel Cover[a] (%)	Hazel Density [b] (stems/m^2)	Hazel CAG[a] (kg/ha)	Shrub Height (cm)	Total Shrub Density (stems/m^2)
Exclosure Location (E)	3	$F = 75.08$	$F = 15.25$	$F = 6.78$	$F = 21.37$	$F = 6.66$
		$p = 0.003$	$p = 0.025$	$p = 0.075$	$p = 0.016$	$p = 0.077$
Boreal		31.7 (3.1)bc	8.0 (0.6)ab	442 (86)b	111.7 (25.1)b	20.6 (1.3)ab
Astotin		80.4 (0.4)a	31.0 (7.9)a	1776 (28)a	166.9 (14.5)a	41.2 (8.05)a
Shirley		38.8 (10.3)b	14.4 (1.05)ab	636 (140)b	128.4 (27.0)b	26.0 (0.8)ab
Tawayik		3.8 (3.2)c	1.2 (0.8)b	260(148)b	109.3 (18.8)b	13.5 (1.05)b
Browsing	1	$F = 0.002$	$F = 0.01$	$F = 0.79$	$F = 55.02$	$F = 0.29$
		$p = 0.9670$	$p = 0.939$	$p = 0.439$	$p = 0.005$	$p = 0.628$
Protected		36.2 (16.63)	15.0 (8.39)	735 (369)	150.43a	26.5 (8.00)
Browsed		41.2 (15.54)	12.3 (4.52)	822 (323)	107.73b	24.1 (3.93)
E x B*	3					

[a], [b] Data transformed prior to analysis using log(y+1) and square root transformations, respectively. Original means presented for clarity.

* Error term for main effects.

**Note:** Within a characteristic and treatment, means with different letters differ significantly (p<0.10).

Table 5.4: Exclosure location, browsing and interaction effects on individual hazel shrub characteristics in 1999 and 2000.

Anova	df	Leaf Phytomass[c] F	Leaf Phytomass[c] P	Twig Phytomass[c] F	Twig Phytomass[c] P	Total Twig Length[c] F	Total Twig Length[c] P	Number of New Twigs[c] F	Number of New Twigs[c] P
1999									
Exclosure Locaiton (E)	3	4.20	0.135	3.12	0.188	3.20	0.182	0.78	0.578
Browsing (B)	1	2.20	0.234	0.33	0.604	0.25	0.651	0.71	0.460
E x B*	3	2.45	**0.066**	4.61	**0.004**	4.26	**0.006**	3.00	**0.032**
Error**	152								
2000									
Exclosure Location (E)	3	0.49	0.711	1.00	0.501	1.44	0.387	0.33	0.805
Browsing (B)	1	0.62	0.487	0.92	0.409	0.17	0.706	2.33	0.224
E x B*	3	6.37	**0.0004**	7.57	**0.0001**	5.56	**0.001**	2.77	**0.044**
Error**	152								

[c] Data transformed prior to analysis using log y transformation.

* Error term for main exclosure and browsing effects.

** Error term for interaction effect.

Table 5.5: Exclosure location, browsing and interaction effects on nutrient composition [mean ± (SE)] of beaked hazel shrubs in 2000.

Anova	df	Twig Crude Protein (%)	Leaf Crude Protein (%)	Twig ADF (%)	Leaf ADF (%)
Exclosure Location (E)	3	$F = 68.78$	$F = 11.98$	$F = 0.11$	$F = 0.88$
		$p = \mathbf{0.003}$	$p = \mathbf{0.036}$	$p = 0.947$	$p = 0.541$
Boreal		4.76 (0.15)b	13.52 (0.45)b	46.20 (0.28)	33.51 (0.71)
Astotin		5.66 (0.26)a	13.08 (0.24)b	46.63 (0.13)	38.59 (0.12)
Shirley		5.96 (0.09)a	10.54 (0.43)c	46.22 (1.33)	35.31 (5.41)
Tawayik		5.09 (0.15)ab	15.26 (0.14)a	46.16 (0.05)	33.99 (0.88)
Browsing (B)	1	$F = 4.98$	$F = 0.57$	$F = 1.38$	$F = 2.13$
		$p = 0.112$	$p = 0.504$	$p = 0.325$	$p = 0.241$
Protected		5.44 (0.19)	12.89 (0.77)	46.69 (0.30)	37.13 (1.55)
Browsed		5.30 (0.23)	13.31 (0.55)	45.92 (0.39)	33.57 (1.78)
E x B*	3	$F = 0.10$	$F = 11.11$	n/a	n/a
		$p = 0.956$	$p = \mathbf{0.003}$		
Boreal protected		4.82 (0.22)	12.81 (0.43)c		
Boreal browsed		4.69 (0.28)	14.22 (0.07)ab		
Astotin protected		5.66 (0.11)	13.40 (0.32)bc		
Astotin browsed		5.67 (0.64)	12.76 (0.16)c		
Shirley protected		6.04 (0.15)	9.84 (0.33)e		
Shirley browsed		5.88 (0.09)	11.23 (0.12)d		
Tawayik protected		5.25 (0.25)	15.49 (0.00)a		
Tawayik browsed		4.94 (0.18)	15.03 (0.13)a		
Error **	8				

* Error term for main exclosure and browsing effects.

** Error term for interaction effect.

Note: Within a characteristic and treatment, means with different letters differ significantly (p<0.10).
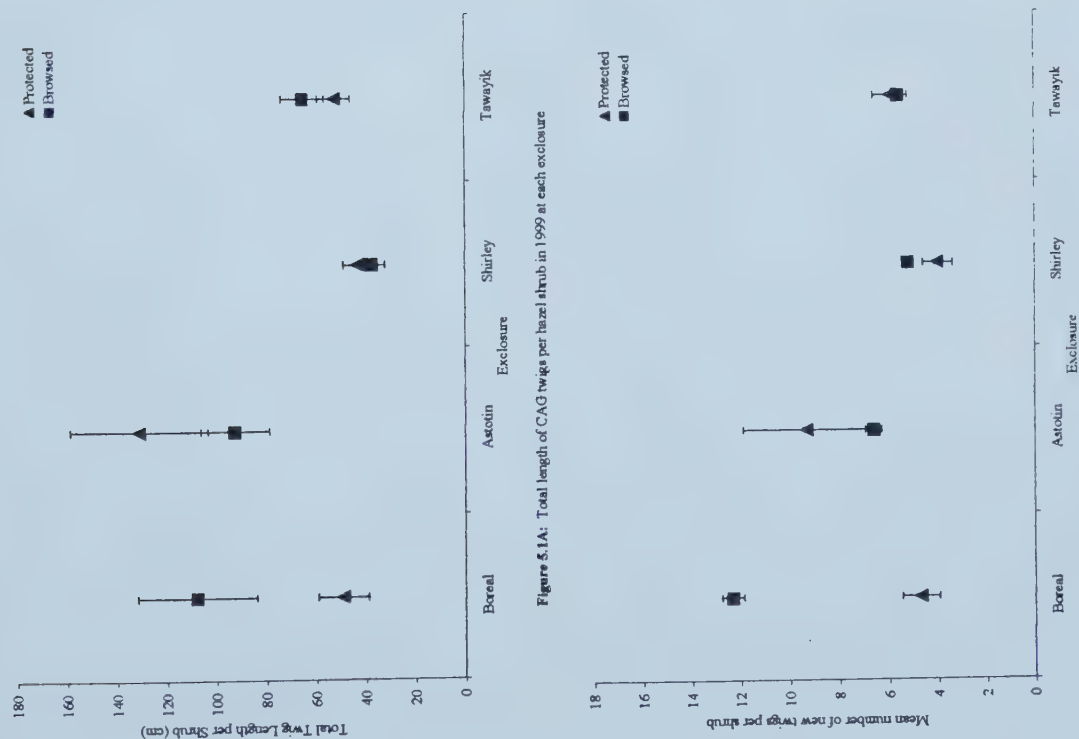
Figure 5.1A: Total length of CAG twigs per hazel shrub in 1999 at each exclosure
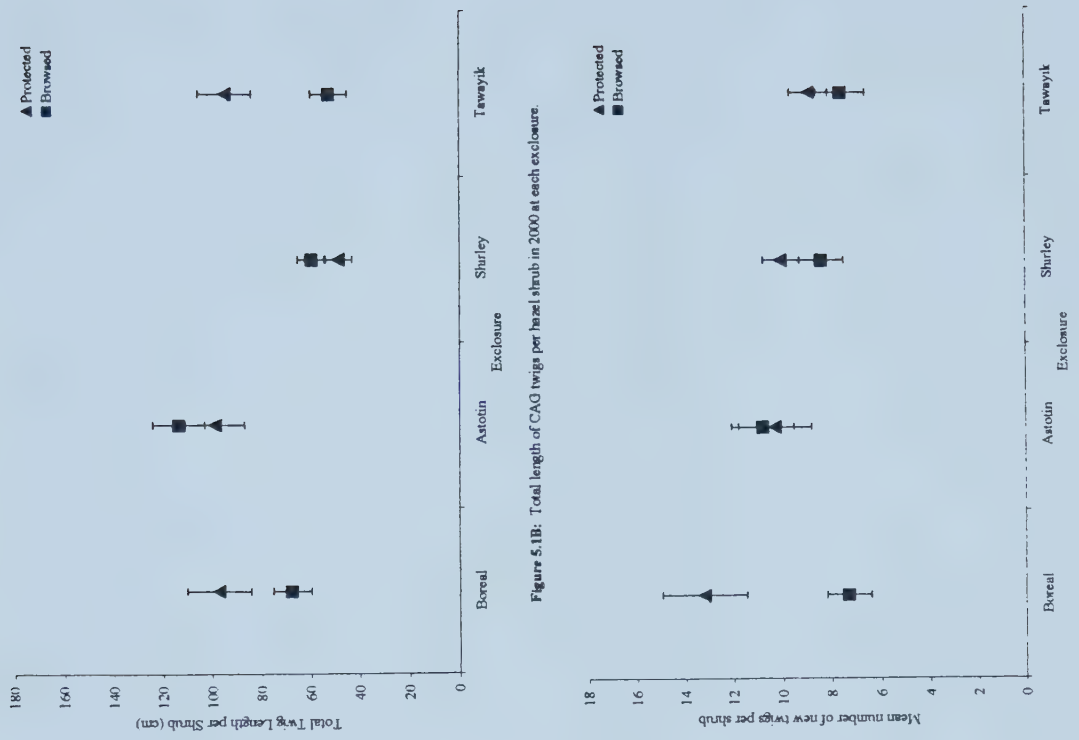
Figure 5.1B: Total length of CAG twigs per hazel shrub in 2000 at each exclosure.
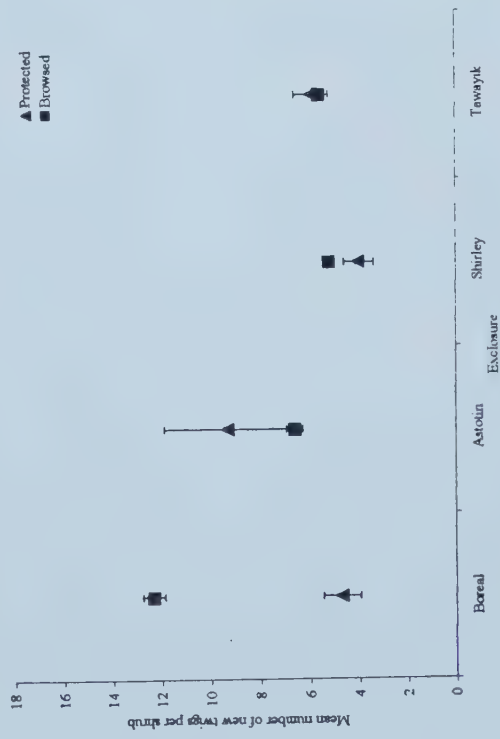
Figure 5.1C: Mean number of twigs per hazel shrub in 1999 at each exclosure
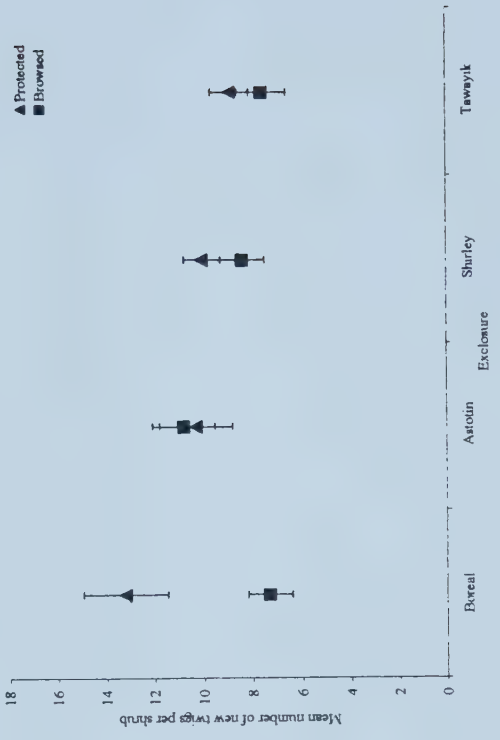
Figure 5.1D: Mean number of twigs per hazel shrub in 2000 at each exclosure

Figure 5.1: Morphological response [mean ± (SE)] of beaked hazel shrubs in EINP to the removal of herbivory (1999 & 2000).
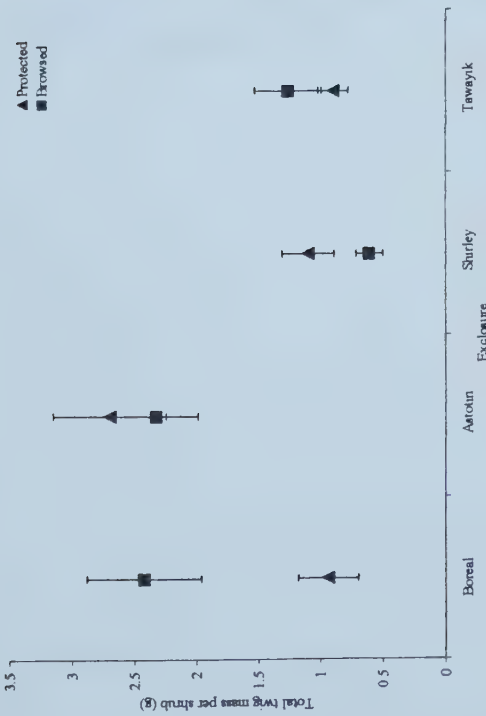
Figure 5.2A: Total twig mass per hazel shrub in 1999 at each exclosure.
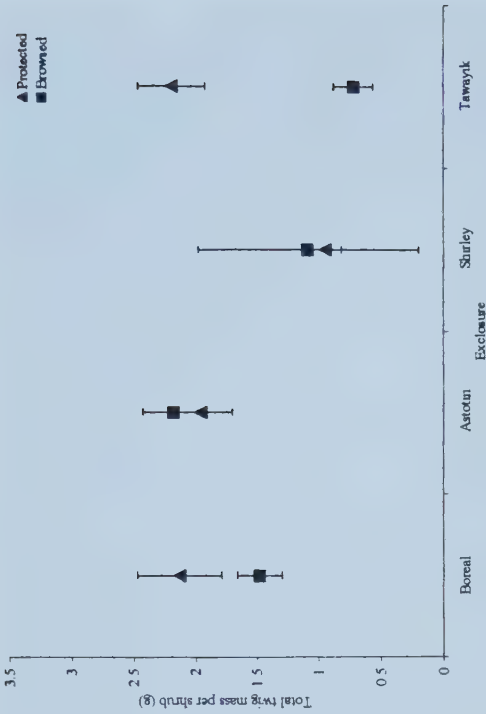
Figure 5.2B: Total twig mass per hazel shrub in 2000 at each exclosure.
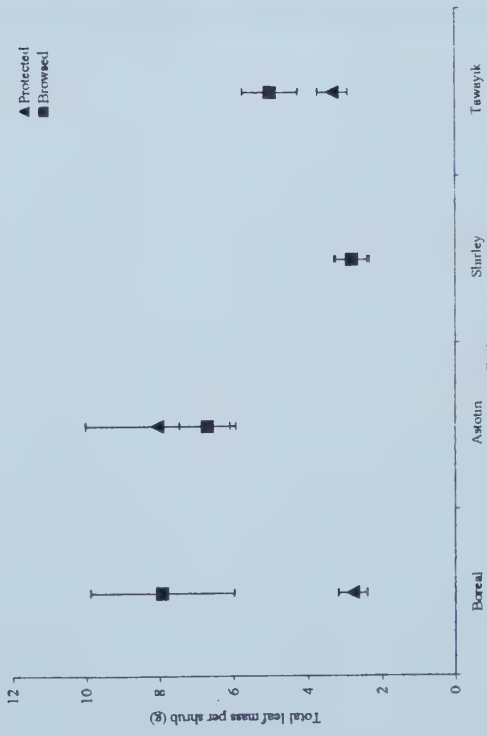
Figure 5.2C: Total leaf mass per hazel shrub in 1999 at each exclosure.
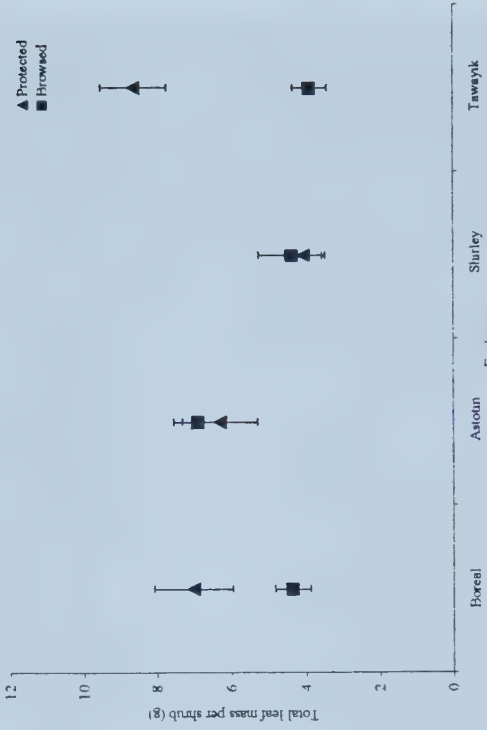
Figure 5.2D: Total leaf mass per hazel shrub in 2000 at each exclosure.

Figure 5.2: Current annual growth (CAG) response [mean ± (SE)] of beaked hazel shrubs in EINP to the removal of herbivory (1999 & 2000).

Figure 5.3: Well-defined browse-line in beaked hazel community outside the Astotin exclosure in EINP (2000).

CHAPTER 6: Synthesis

When Elk Island National Park was established in 1906 it was to preserve one of the last remaining elk herds in the area (Blyth 1995). Since then, large herds of bison, elk and moose have proliferated within the Park and placed great demand on the forage resource. Due to the fenced nature of the Park, the visibility of large herbivores, and public concern over their well-being, Park managers have traditionally been forced to focus large ungulates (Blyth 1995) while the habitat resource has been somewhat overlooked. The National Parks Act (Parks Canada 1988), however, identified the preservation and protection of biodiversity and ecological integrity as a major goal for national parks. Recently, EINP staff have developed a process-based management philosophy in an effort to integrate this mandate into park management (Cool 1999). Two of the main ecological processes identified in EINP are herbivory and fire.

Elk Island National Park is thought to be part of the transition from the Aspen Parkland to the Boreal Mixedwood Forest. Elk, moose and deer were historically common to the area. Bison also used the habitat within the Park as wintering grounds before European settlement. Annual migration patterns indicate that bison preferred open prairie during summer, and Aspen Parkland during winter (Baumeister et al. 1996; Morgan 1980). These migrations suggest that grazing pressure from bison, at least during the summer, was low in EINP prior to its inception. Upon creation of the Park, major predators were eradicated from the area, an ungulate-proof perimeter fence was built, and hay was supplied to the bison in winter (Blyth 1995). These conditions abruptly changed forage utilization patterns, placing high demands on the forage resource during the summer (when the bison joined the other ungulates to forage in what used to be winter

habitat) and winter (since the fence precluded ungulate movement and predators did not exist to control growing ungulate populations). In addition, the suppression of wildfire within the Park may have contributed to changes in vegetation, particularly increases in aspen forest establishment as has been documented elsewhere (Scheffler 1976; Bailey and Wroe 1974).

Bork et al. (1997a, 1997b) documented changes in vegetation composition and structure resulting from intensive year-long ungulate herbivory within the Park. In general, the height of the forest understory was reduced, and plant communities changed towards an increasing abundance of shorter, exotic herb species (e.g., *Poa pratensis* L. and *Taraxacum officinale* Weber) and browsing tolerant shrubs (e.g., *Corylus cornuta* Marsh) (Bork et al. 1997a).

Currently, Park managers maintain native ungulate numbers by removing some ungulates each year. However, the number of animals removed is only slightly above projected herd increases (EINP 1999) with the result that grazing pressure remains somewhat constant. In addition, bison and elk are supplemented with hay during winter, which has the potential to increase herd size indirectly by improving herd health and reproduction rates. Prescribed fire has also been introduced to the Park to reduce forest cover and, in doing so, provide more "suitable" habitat for native ungulates.

In this research, limited changes in plant community composition and structure were found immediately following short-term (e.g., 2 year) exclusion of ungulate herbivory. Specifically, shrub height and herb production increased on protected sites, while no changes were observed in species composition, including within the non-native (invasive) component of plant communities (Chapter 3). In addition, beaked hazel, the

dominant shrub and key browse species within the Park, was found to be detrimentally affected by high ungulate stocking rates (Chapter 5). While its response to the removal of browsing varied with location, beaked hazel production generally appears to be depressed under current levels of browsing. Other plant species indigenous to the Park have been threatened with extirpation by heavy levels of herbivory. Bork et al. (1997b) documented a lack of mature saskatoon and chokecherry shrubs, while Blyth et al. (1993) noted that plains rough fescue only occurred at one location in EINP. My results indicate that plant community resilience to previous levels of herbivory is low, further threatening the long-term biodiversity and ecological integrity of the Park's natural resources. This supports the contention of Bork et al. (1997a) that rangelands in EINP have exceeded a threshold and recovery from intense grazing (accompanied by invasion by exotic species) may be limited without active rehabilitative measures – a situation also observed by Trottier (1986) in Riding Mountain National Park.

This stated, let's examine the worst case scenario. In the future, if ungulate management within the Park remains the same the symptoms of overgrazing may become more pronounced and the loss of ecological integrity and biodiversity may become greater and be even more likely to be permanent. More specifically, year-long heavy grazing may continue to promote invasion by exotic species and reduce the vigour and abundance of native plant species. Hay used to supplement bison and elk winter diets may also continue to increase exotic species within the Park by distributing seeds of exotic species. Bare soil, soil pH, and soil temperature may increase, while soil moisture and organic matter decrease (Johnston et al. 1971), resulting in significant changes to microclimate that reduce the potential for native plant community recovery. Shrub

density, cover and production may continue to be reduced by heavy browsing. Forest cover may decrease as aspen stands become decadent and regenerating aspen suckers are killed by intense browsing. In summary, the loss of habitat and vegetative cover, as well as reduced forage production may to continue if current levels of intense ungulate herbivory persist. In the extreme, this could result in extensive permanent damage to the Park's ecosystems, as well as starvation and ungulate population die-offs in the long-term.

It is important to note that these possibilities do not reflect a previous lack of sensitivity, nor initiative on behalf of Park managers, but rather a lack of resources and management alternatives to deal with ungulate populations. In the past, controlled slaughters and contraceptives were employed to limit ungulate numbers, neither method is permitted today.

Currently, several options are available to try to restore biodiversity and ecological integrity within the Park. These include, but are not limited to, significant reductions of ungulate populations through live trapping, the use of prescribed fire, and plant community rehabilitation (e.g., seeding or transplanting). The ideal recovery program is likely to include a combination of these three activities because, as observed here, the short-term response to the removal of herbivory indicates that plant community resilience is low (Chapter 3). Careful long-term monitoring of rangelands will also be a valuable tool to Park managers in evaluating the extent of native plant community recovery.

A significant reduction in ungulate populations would reduce grazing pressure throughout the Park and may permit recovery of some plant species, as well as facilitate

increases in structural diversity (Chapter 3). However, reduced grazing alone may fail to facilitate the replacement of exotic species with native species and restore ecosystem function.

Other studies have found fire to be useful in reducing exotic species (Towne and Owensby 1984), especially Kentucky bluegrass, which is dominant on uplands in EINP. Fire also has the potential to increase nutrient cycling and alter plant community composition by changing range site potential (Volesky and Connot 2000; Redman et al. 1993; Bailey and Anderson 1978), as well as promote the regeneration of aspen and shrub layers (Romo et al. 1993; Johnston and Woodard 1985; Anderson and Bailey 1980). While the use of fire alone to improve ecological integrity may result in increased herbivore utilization of burned areas, fire in conjunction with reductions in ungulate numbers may minimize this effect and promote native plant community recovery. Additional research is needed to evaluate the effect of fire and the interaction of fire and herbivory on biodiversity and ecological integrity in EINP.

In addition to effective management of herbivory and fire, more intensive species specific measures may be required to facilitate the recovery of key plant species within the Park. Active rehabilitation (e.g., seeding, transplanting, etc.) is an expensive, labour intensive endeavour that has the potential to increase native biodiversity. For those plant communities heavily dominated by exotic species, rehabilitation may be the only way to re-establish plant species that have been locally extirpated from regions of the Park (Trottier 1986; Willoughby 1997). For example, plains rough fescue is thought to have been a dominant grass species and is now found at only one location within the Park (Blyth et al. 1993). Evaluation of transplanted plains rough fescue survival and vigour on

grazed and ungrazed sites indicates that current levels of herbivory in the Park reduce fescue establishment and growth in the short-term, and may lead to increased fescue mortality in the future (Chapter 4). To maximize the establishment of transplanted plains rough fescue, stocking rates within the Park would need to be reduced. Prescribed burning may also benefit fescue re-establishment by limiting competition from exotic species and encroaching shrub and forest vegetation. However, before fescue is considered for large-scale re-establishment, its presence as a dominant historical species within the Park should be confirmed.

In summary, it is likely that to promote native biodiversity and ecological integrity within EINP, native ungulate numbers need to be reduced and ungulate utilization patterns (e.g., feeding hay in winter, and grazing of Aspen Parkland in spring and summer) changed to more closely resemble historical migration patterns. If native species recovery is a primary goal [as stated in the National Parks Act (Parks Canada 1988)], plant material (e.g., hay) should not be brought into the Park except for tightly controlled rehabilitative measures such as native plant seeding and transplantation efforts. Similarly, innovative grazing systems/patterns may have to be introduced to ensure protection of the long-term integrity of native plant communities.

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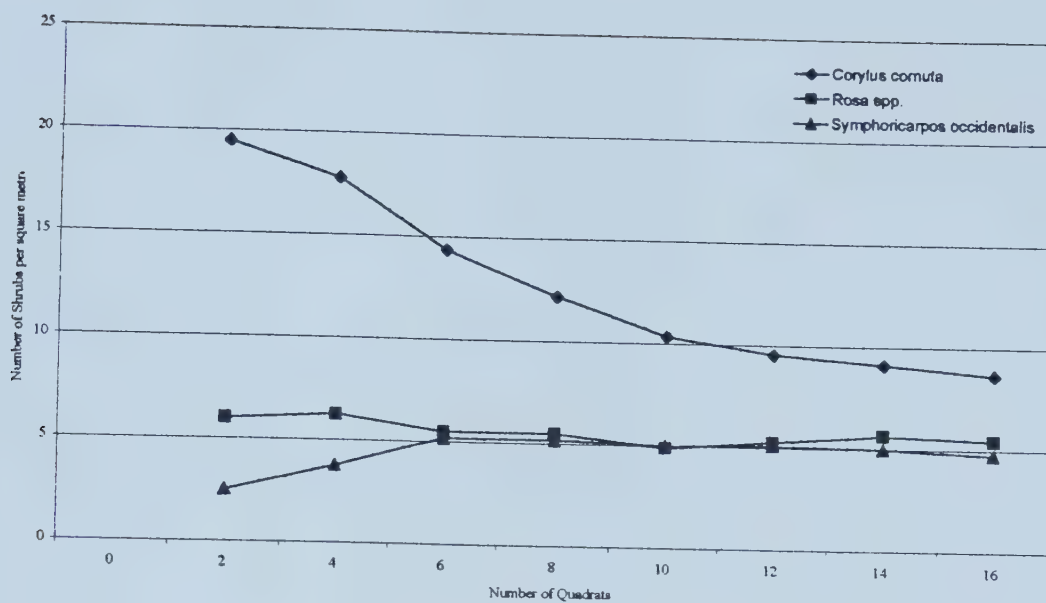
APPENDIX 1: Sample Size Pilot Studies
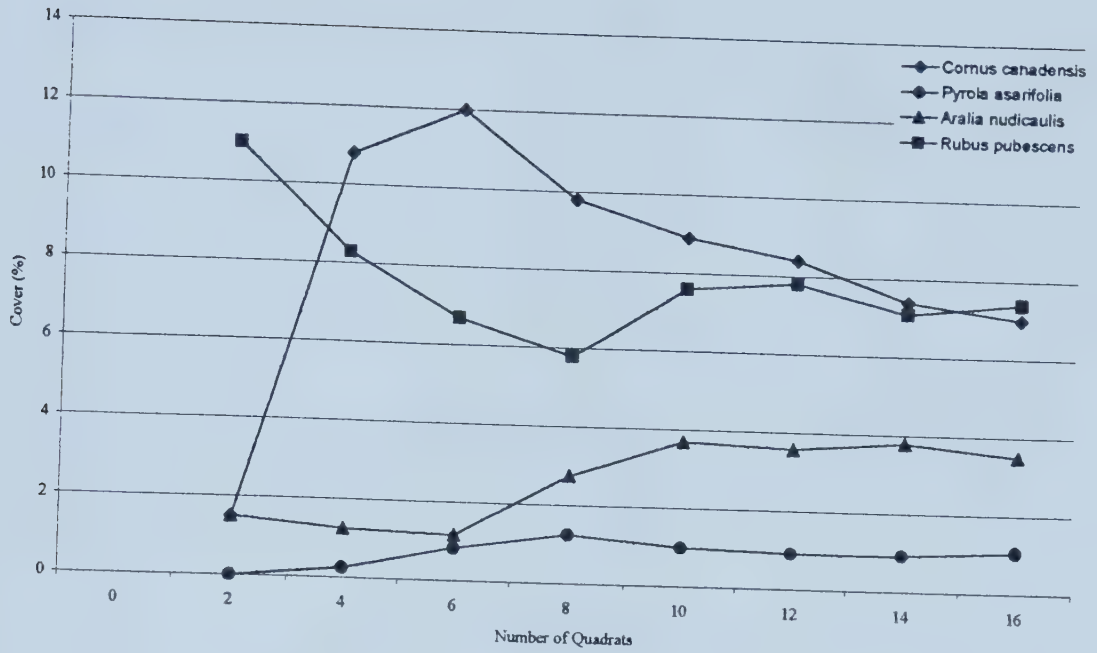
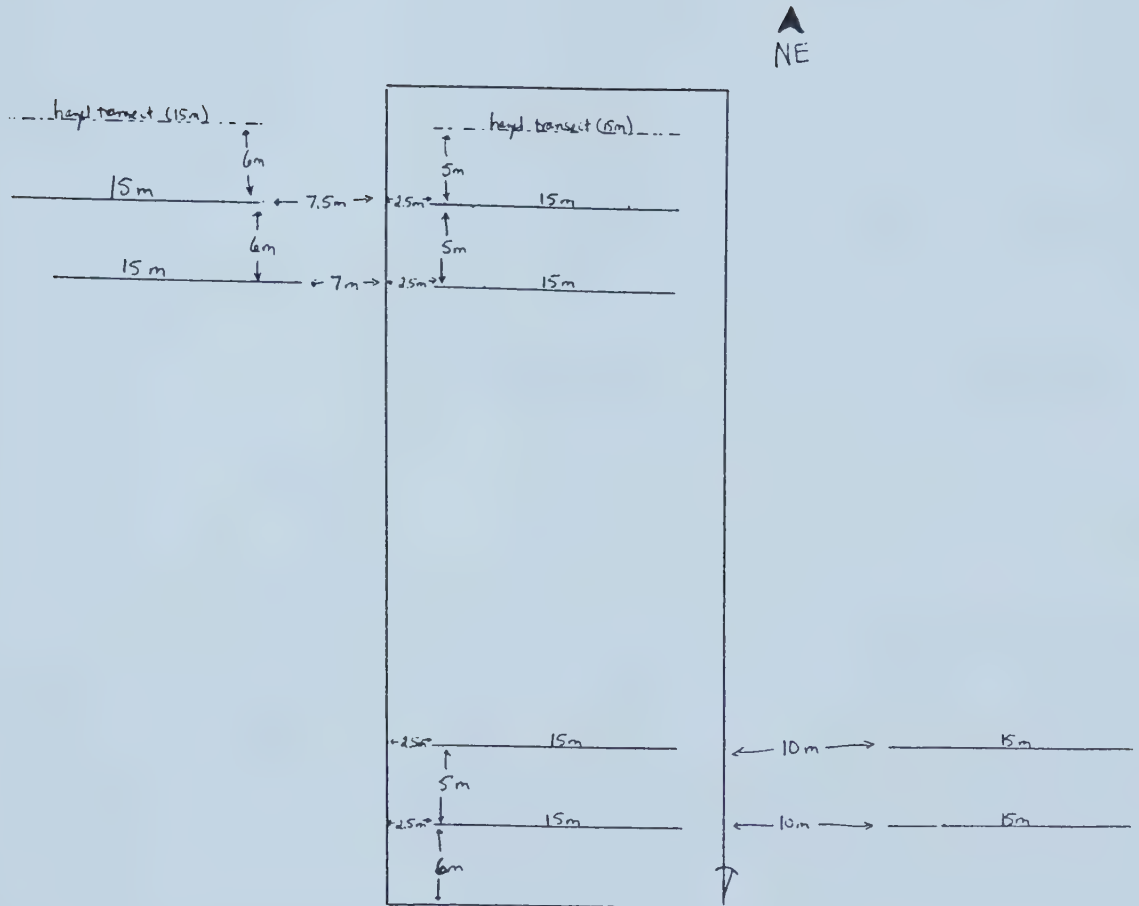Pilot study running averages for species cover on north-facing slopes.
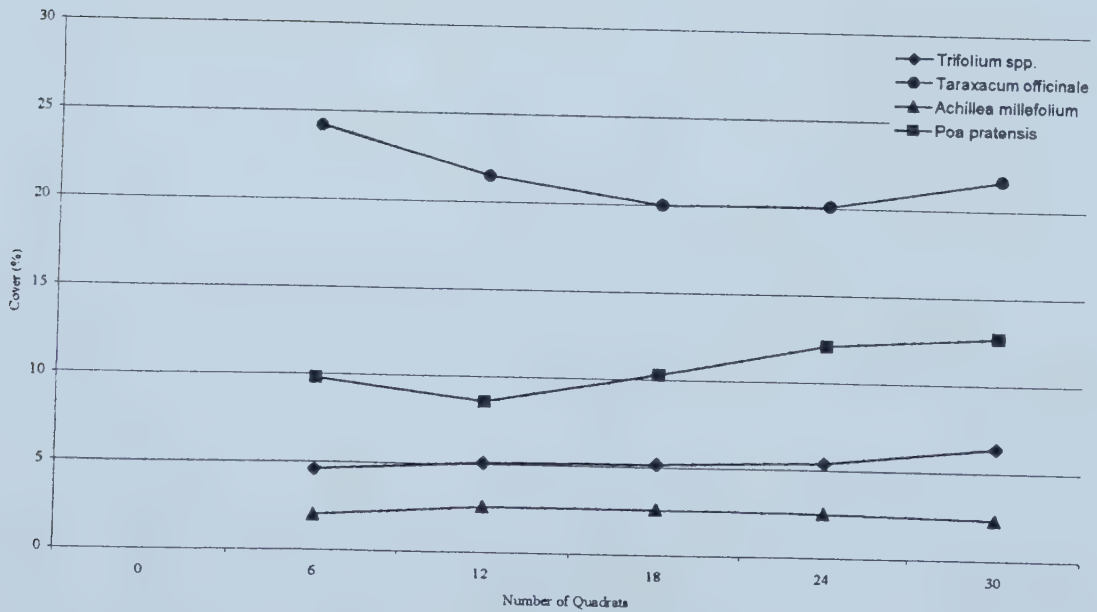
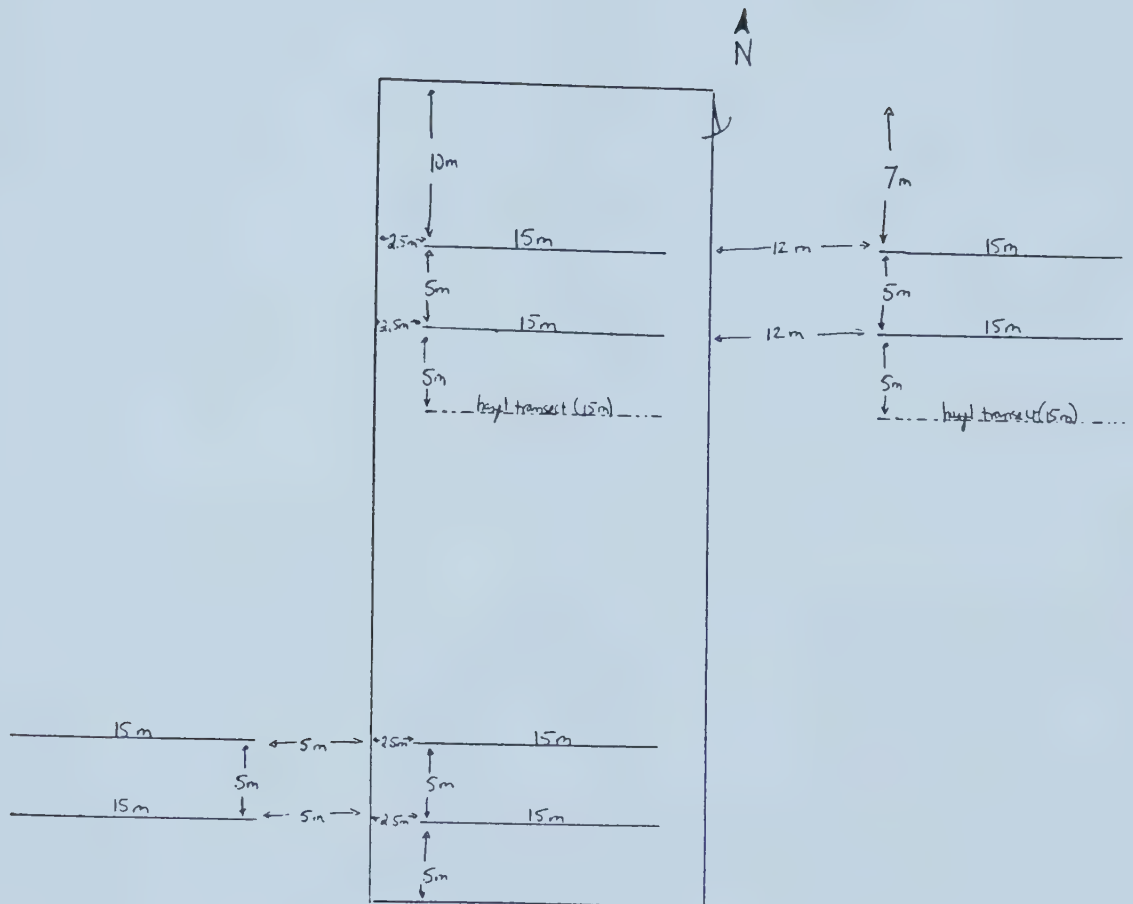Pilot study running averages of grassland species cover.

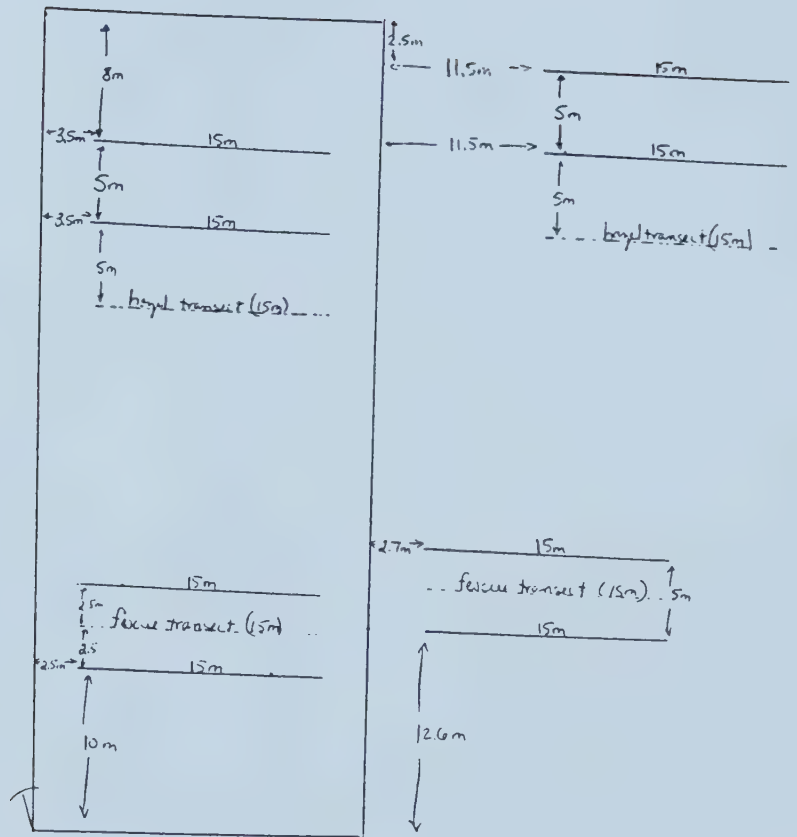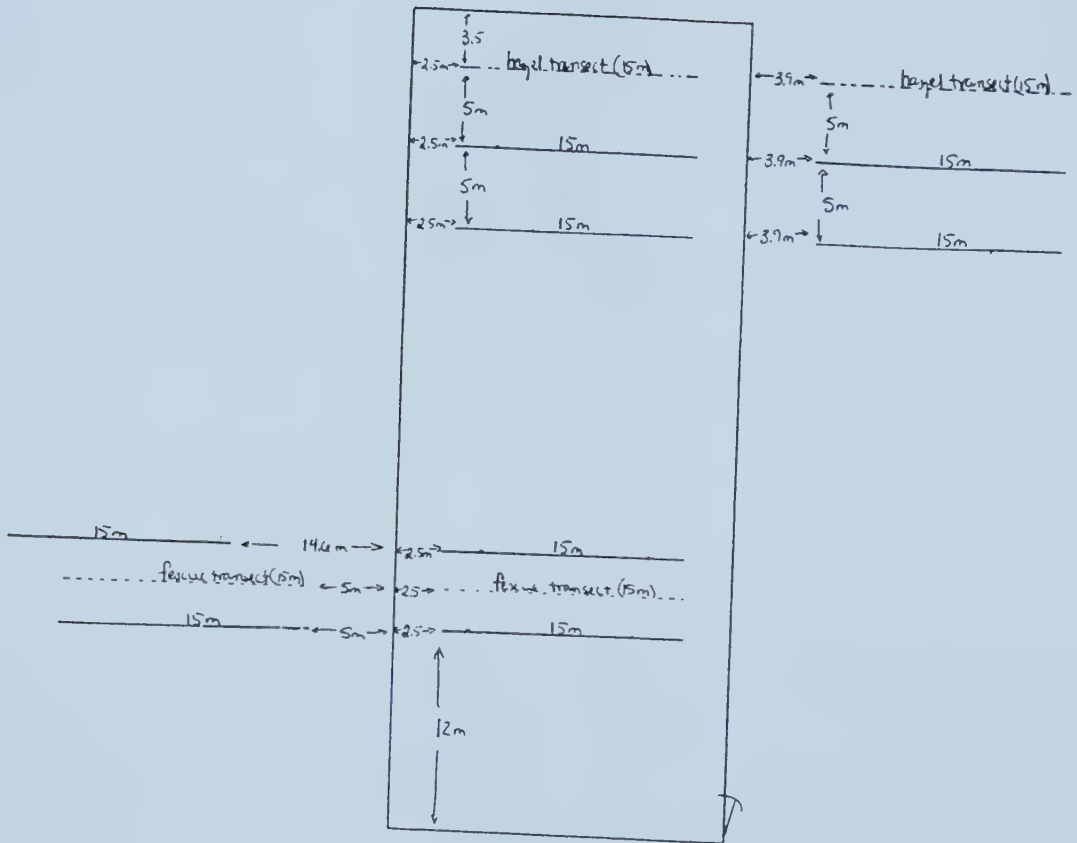Pilot study running averages for shrub density.
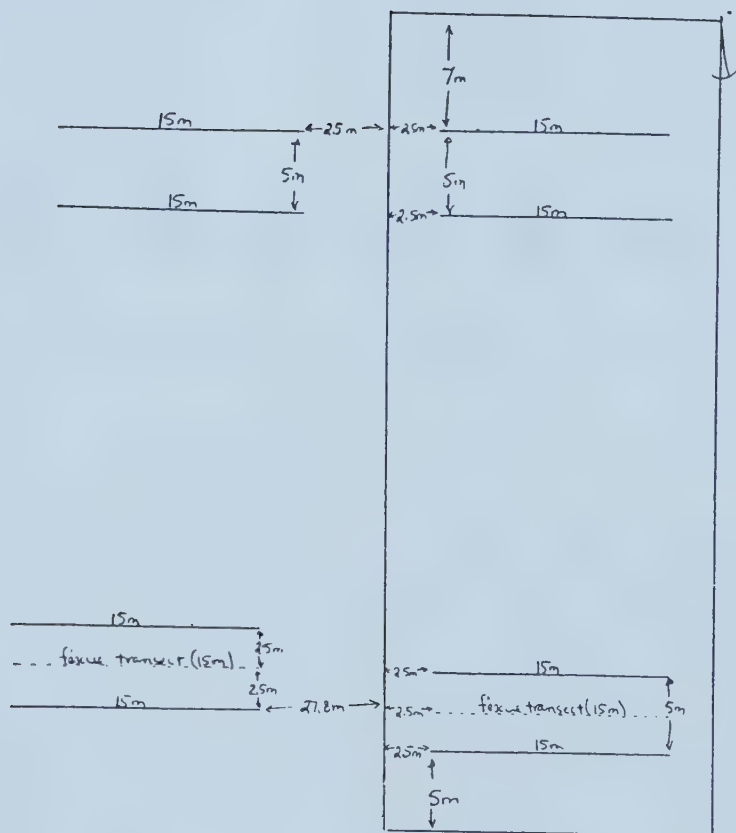
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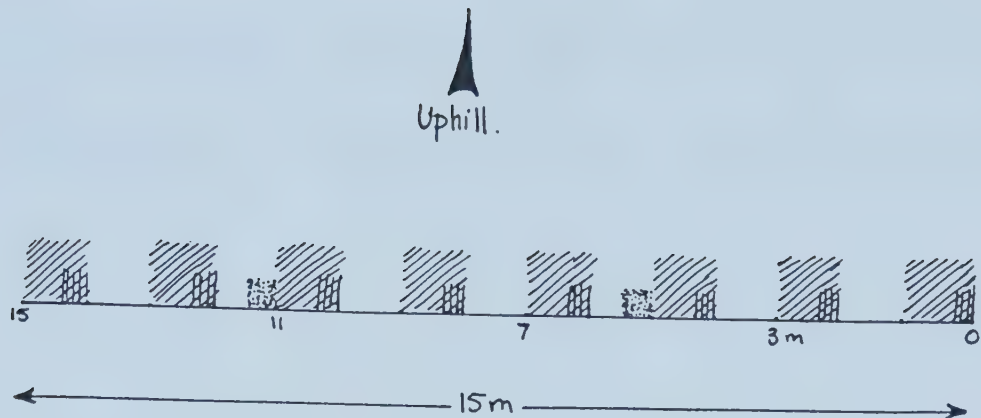

Astotin Exclosure

Boreal Exclosure

Shirley Exclosure

Tawayik Exclosure

Ranger Exclosure

Bailey Exclosure

Uphill.

15   11   7   3 m   0

15 m

▨ shrub density, shrub cover, shrub height. (1 m²).
▩ spp. cover, herbage height (0.4 x 0.5 m).
▦ clip plots (0.25 m²).

Species composition transect lay-out

Location of transplanted plains rough fescue

Shirley Protected (metres from west fence): 3.6, 4.7, 5.7, 7, 8.3, 9.6, 11.4, 12.4, 14.1, 15.1
Shirley Grazed (metres from east fence): 3, 4.5, 6.1, 7.4, 9.2, 10.6, 12, 14.1, 15.2, 17.1

Tawayik Protected (metres from east fence): 2.6, 4, 5.5, 7, 8.5, 10, 11.5, 13, 14.5, 16
Tawayik Grazed (metres from east peg): 1.22, 4.2, 5.3, 6.2, 7.1, 8.7, 10.3, 11.5, 13, 14.5

Bailey Protected (metres from east fence): 3.2, 4.2, 5.5, 7, 8.5, 10.4, 11.5, 13, 14.9, 16.6
Bailey Grazed (metres from east peg): 0.5, 2, 3.5, 5, 6.5, 8, 9.5, 11, 12.5, 14

Ranger Protected (metres from west peg): 0.6, 1.5, 2.6, 4.9, 6.8, 8.7, 9.9, 12.2, 13.5, 14.4
Ranger Grazed (metres from east peg): 0.5, 2, 3.5, 5, 6.5, 8, 9.5, 11, 12.5, 14

APPENDIX 3: List of Plant Species Found in and Adjacent to Exclosures in 1999 and 2000

Achillea millefolium L.	Common yarrow
Actaea rubra (Ait.) Willd.	Red & white baneberry
Agastache foeniculum (Pursh) Ktze.	Giant hyssop
Agrimonia striata Michx.	Agrimony
Agropyron hybrid	Wheatgrass hybrid
Agropyron repens (L.) Beauv.	Quackgrass (I)
Agropyron trachycaulum var. trach. (Link) Malte	Slender wheatgrass
Agropyron trachycaulum var. uni. (Cassidy) Malte	Bearded wheatgrass
Agrostis stolonifera L.	Redtop (I)
Amelanchier alnifolia Nutt.	Saskatoon berry
Anemone canadensis L.	Canada anemone
Antennaria parvifolia Nutt.	Small-leaved pussytoes
Apocynum androsaemifolium L.	Spreading dogbane
Aralia nudicaulis L.	Wild sarsparilla
Arctostaphylos uva-ursi (L.) Spreng.	Common bearberry
Arenaria lateriflora L.	Blunt-leaved sandwort
Aster ciliolatus Lindl.	Fringed aster
Aster conspicuus Lindl.	Showy aster
Aster laevis L.	Smooth aster
Aster puniceus L.	Purple-stemmed aster
Betula papyrifera Marsh.	Paper birch
Bromus ciliatus L.	Fringed brome
Bromus inermis Leyss.	Smooth brome
Calamagrostis canadensis (Michx.) Beauv.	Marsh reed grass
Campanula rotundifolia L.	Bluebell
Carex spp.	Sedge
Castilleja miniata Mutis *ex* L.f.	Indian paint-brush
Cirsium arvense (L.) Scop.	Canada thistle
Cornus canadensis L.	Bunchberry
Cornus stolonifera Michx.	Red-osier dogwood
Corylus cornuta Marsh.	Beaked hazelnut
Crataegus rotudifolia Moench	Hawthorn
Danthonia californica Boland	Intermediate oatgrass
Disporum trachycarpum (S. Wats.) B. & H.	Fairybells
Elymus innovatus Beal	Hairy wild rye
Epilobium angustifolium L.	Fireweed
Equisetum arvense L.	Common horsetail
Equisetum hyemale L.	Common scouring rush
Equisetum pratense Ehrh.	Meadow horsetail
Equisetum sylvaticum L.	Woodland horsetail

* (I) indicates species that were classified as introduced.

Erigeron glabellus Nutt.	Smooth fleabane
Erigeron philadelphicus L.	Philadelphia fleabane
Festuca hallii (Vasey) Piper	Plains rough fescue
Festuca saximontana Rydb.	Sheep fescue
Fragaria virginiana Duchesne	Wild strawberry
Galeopsis tetrahit L.	Hemp-nettle
Galium boreale L.	Northern bedstraw
Galium triflorum Michx.	Sweet-scented bedstraw
Geranium bicknellii Britt.	Bicknell's geranium
Geum aleppicum Jacq.	Yellow avens
Geum rivale L.	Purple avens
Geum triflorum Pursh	Three-flowered avens
Halenia deflexa (Sm.) Griseb.	Spurred gentian
Heracleum lanatum Michx.	Cow parsnip
Hieracium umbellatum L.	Narrow-leaved hawkweed
Lathyrus ochroleucus Hook.	White peavine
Lathyrus venosus Muhl.	Purple peavine
Ledum groenlandicum Oeder	Common Labrador tea
Lilium philadelphicum L.	Tiger lily/Western wood lily
Linnaea borealis L.	Twinflower
Lonicera dioica L.	Twinning honeysuckle
Lonicera involucrata (Richards.) Banks	Bracted Honeysuckle
Maianthemum canadense Desf.	Wild lily-of-the-valley
Melilotus alba Desr.	White sweet clover (I)
Melilotus officinalis (L.) Lam.	Yellow sweet clover (I)
Mertensia paniculata (Ait.) G. Don.	Tall lungwort
Mitella nuda L.	Bishop's cap
Oryzopsis pungens (Torr.) A.S. Hitchc.	Northern ricegrass
Petasites palmatus (Ait.) A. Gray.	Palmate-leaved coltsfoot
Petasites sagittatus (Pursh) A. Gray.	Arrow-leaved Coltsfoot
Phleum pratense L.	Timothy (I)
Plantago major L.	Common plantain (I)
Poa pratensis L.	Kentucky bluegrass (I)
Populus balsamifera L.	Balsam poplar
Populus tremuloides Michx.	Trembling aspen
Potentilla anserina L.	Silverweed
Potentilla gracilis Dougl. *ex* Hook.	Graceful cinquefoil
Primula incana M.E. Jones	Mealy primrose
*Prunus virginiana*L.	Chokecherry
Prunus pensylvanica L.f.	Pincherry
Pyrola asarifolia Michx.	Common pink wintergreen
Pyrola chlorantha Sw.	Green wintergreen
Ribes americanum Mill.	Wild black currant.
Ribes oxyacanthoides L.	Wild gooseberry
Ribes triste Pall.	Wild red currant
Rosa woodsii Lindl.	Common wild rose

Rubus idaeus L.	Wild red raspberry
Rubus pubescens Raf.	Dewberry
Salix spp.	Willow
Sanicula marilandica L.	Snakeroot
Schizachne purpurascens (Torr.) Swallen	Purple oat grass
Scutellaria galericulata L.	Marsh skullcap
Senecio eremophilus Richards.	Cut-leaved ragwort
Shepherdia canadensis (L.) Nutt.	Canada buffaloberry
Sisyrinchium montanum Greene	Common blue-eyed grass
Smilacina stellata (L.) Desf.	Star-flowered false Solomon's seal
Solidago canadensis L.	Canada goldenrod
Solidago spathulata DC.	Mountain goldenrod
Sonchus arvensis L.	Perennial sow thistle
Stachys palustris L.	Marsh hedge-nettle
Stellaria longifolia Muhl.	Long-leaved chickweed
Stellaria media (L.) Cyrill.	Common chickweed
Symphoricarpos occidentalis Hook.	Western snowberry
Taraxacum officinale Weber	Common dandelion (I)
Thalictrum venulosum Trel.	Veiny meadow rue
Trifolium hybridum L.	Alsike clover (I)
Trfolium repens L.	White clover (I)
Urtica dioica L.	Stinging nettle
Vaccinium vitis-idaea L.	Bog cranberry
Vaccinium myrtilloides Michx.	Common blueberry
Viburnum edule (Michx.) Raf.	Low-bush cranberry
Vicia americana Muhl.	Wild vetch
Viola adunca J.E. Smith	Early blue violet
Viola canadensis L.	Western Canada violet